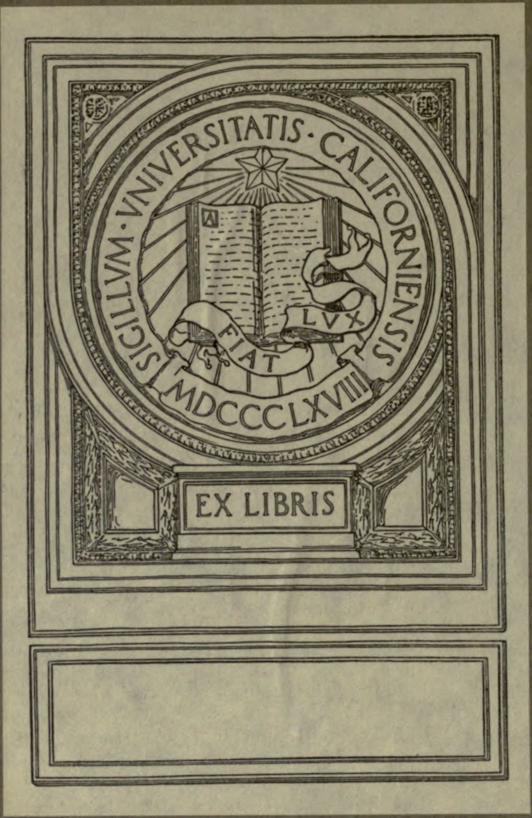

MEMOIRS
OF THE
UNIVERSITY OF CALIFORNIA

Vol. 1. No. 1

TRIASSIC ICHTHYOSAURIA

WITH SPECIAL REFERENCE TO THE AMERICAN FORMS

BY
JOHN C. MERRIAM

BERKELEY
THE UNIVERSITY PRESS
1908

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INTRODUCTION.

In a series of short papers appearing at irregular intervals since 1895, the writer has attempted to present some of the more important facts relating to the structure and occurrence of certain of the American Triassic Ichthyosauria. In the earlier stages of this work the known material was scanty and generally fragmentary, and it has not been possible in every case satisfactorily to determine the structure or the exact relationships of forms described. With a great increase in the quantity of material in the last few years, it seems advisable to bring together all available information relating to the American genera, and to consider this body of fact in relation to what is known of the earliest ichthyosaurs of other regions, as also in relation to the general problem of the evolution of this peculiar reptilian order.

Some of the questions here discussed might be considered to better advantage by workers more intimately acquainted with the extensive collections of European ichthyosaur material. The writer has, however, been emboldened to attempt generalizations bearing on the work of other investigators in this field, after consideration of the fact that the West-American collections at the present time seem to represent the largest part of the known Triassic material, and that as yet no other investigator has examined both the European and the American collections.

The investigation has been considerably delayed by the discovery of a new group of marine reptiles, the Thalattosauria, which it was necessary to understand before the true ichthyosaurian remains could be satisfactorily separated for study. Continued discoveries of ichthyosaurian material have also made it advisable to postpone publication until the new specimens could be examined. Even in its present stage the paper here presented can be considered as no more than a report of progress, as new material and additional information regarding the structure and affinities of the Triassic forms are constantly being obtained.

The material upon which the studies of the American Triassic ichthyosaurs are based includes over fifty specimens, each of which represents a considerable part of the skeleton; also a large quantity of more fragmentary material. These collections have been brought together by ten expeditions sent out by the University of California between 1901 and 1907. The material now at hand has been accumulated and made available for scientific study largely through the unflagging interest of Miss Annie M. Alexander, who has furnished the financial support for nearly all of the expeditions, and has most energetically assisted in insuring their success. The largest share of the direction of field work has been carried by Mr. E. L. Furlong, who has also prepared and mounted practically all of the specimens represented in the illustrations of Californian material in this paper.

In the initial stages of the work the writer was greatly indebted to President Benjamin Ide Wheeler of the University of California, through whose support it was made possible to extend the scale of the investigation so as to cover the broader field of the evolution of the Ichthyosauria as a whole.

In the field work carried on in connection with the investigation of the occurrence and age of the Triassic ichthyosaurs, the writer has been particularly indebted to Professor James Perrin Smith, whose knowledge of the invertebrate faunas has furnished a most valuable basis for correlation.

While working on the Ichthyosauria the writer has on several occasions visited nearly all of the American museums in which material of this group is available. The principal collections of European Jurassic ichthyosaurs have also been reviewed, and most of the described specimens from the European Triassic were examined.

In the course of this investigation the writer has been indebted to a number of the principal museums of this country and of Europe for the use of comparative material. For courteous co-operation in farthering the work of comparison, the writer is especially grateful to Dr. A. Smith Woodward and Dr. C. W. Andrews of the British Museum of Natural History; to Professor E. Fraas of the Königliches Naturalien-Cabinet in Stuttgart; and to Dr. F. von Huene and Professor E. Koken of the Geologisch-mineralogisches Institut in Tübingen. The use of several valuable specimens in the museum of the Polytechnikum at Zürich, was kindly permittedby Professor Albert Heim; Dr. W. J. Holland kindly allowed the use of a photograph of the remarkably complete ichthyosaurian specimen in the collections of the Carnegie Museum. In working over the subject of evolution of the Ichthyosauria as a whole, the use of the collections of *Baptanodon* material in charge of Mr. W. H. Reed at the University of Wyoming, and of the types described by Mr. Gilmore at the Carnegie Museum, has been particularly helpful.

The majority of the drawings represented in the plates, also a number of the text figures, were prepared by Mrs. Grace Ballantine. The larger portion of the text figures and several of the plates, including most of the representations of vertebrae, were drawn by Mr. A. J. Heindl.

JOHN C. MERRIAM.

UNIVERSITY OF CALIFORNIA,
FEBRUARY, 1908.

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HISTORICAL REVIEW OF LITERATURE.

The earliest reported discoveries of Triassic ichthyosaurian remains were made known by Herman von Meyer and by G. Curioni in 1847. The material available for von Meyer's studies consisted of a few teeth and vertebrae, and an imperfect sketch of a saurian found at Reiflingen in Steyermark in 1843 by Professor Pranger. Von Meyer knew also of a vertebra from Ettersberg near Weimar. These specimens were mentioned by von Meyer principally because of their occurrence in beds considerably older than those in which the typical ichthyosaurs were known. Nothing particularly characteristic was noted in their structure, and the Reiflingen specimen was compared with Cuvier's figured specimens described as *Ichthyosaurus platyodon.*

In the same year in which von Meyer announced his discovery of Triassic ichthyosaurian remains, G. Curioni gave notice of the occurrence in the bituminous shales of Besano, of a form which he referred to *Ichthyosaurus communis.*

In 1852 fragmentary specimens from the Wellendolomit of the Black Forest, including a vertebra, some paddle bones, and a jaw fragment with teeth, were described under the name of *Ichthyosaurus atavus* by Quenstedt.

In 1855 von Meyer described from the Muschelkalk of Ober-Schlesien a vertebra which resembled a dorsal of an ichthyosaurian. In connection with the description of this specimen reference was made to a somewhat similar vertebra described (Palaeontographica Bd. 1, p. 253, Taf. 29, fig. 55) from Larishof in Ober-Schlesien. This vertebra seemed to show a natural perforation of the centrum. Accompanying it there is figured a vertebra with a central perforation of the centrum, and with a broad unexcavated margin surrounding the deeply concave middle region of the articular face. In 1856 von Meyer gave a brief description of two vertebrae from the Koessner beds of Schleimser Joch in Achenthal and noted their resemblance to *Ichthyosaurus tenuirostris.* Up to this time no evidence had been obtained which tended to show that the Triassic forms were materially different from the typical Jurassic ichthyosaurs.

In 1868, and before the true nature of any European Triassic ichthyosaurian had been made clear, Leidy described the first known specimens from America. Though the material at Leidy's command was very fragmentary, the distinguishing characters of the type they represent could have been made out had some of the enveloping limestone been removed. The characters referred to in the original description were principally those of ordinal value.

In 1873 Hulke described the first ichthyosaurian remains known from Spitzbergen, referring them to *Ichthyosaurus*, of which two species, *I. polaris* and *I. nordenskiöldii* were described. It is apparent from Hulke's description that the single-headed character of the ribs in the dorsal region was recognized, but no special value was assigned to it. The same material was worked over again by Dames in 1895, and assigned to the genus *Mixosaurus*. Curiously enough, Dames failed to accept the statement that single-headed ribs of this character occurred in *Shastasaurus*, and assumed that the ribs must be double-headed as in *Mixosaurus*, of which he appears to have had little available information.

In 1873 Sauvage described from the Rhaetic of Saone-et-Loire in France two types of vertebrae designated as *Ichthyosaurus rheticus* and *I. carinatus*. In 1876 these species were figured and more fully described by Sauvage, there being, however, only fragmentary material available. In the same publication, Sauvage described under the name *Rachitrema pellati* a form represented by a vertebral arch, a scapula, and several fragmentary arch and limb bones. *Rachitrema* was referred by Sauvage to the Dinosauria, but was later referred to the Ichthyosauria.

The description of a Triassic ichthyosaurian species, *Ichthyosaurus cornalianus*, from the bituminous shales of Besano in northern Italy, by Bassani in 1886, marked the beginning of the first studies of the forms in which sufficient material was available for satisfactory investigation of the skeletal characters.

In 1887, shortly after the description of the Besano specimen by Bassani, Baur (1877, 1) published his brief but important note on the structure of the limbs of the Italian specimens. It was then for the first time clearly shown that the ichthyosaurian limb in the Triassic stage of development was much farther away from the fish type than were the limbs of the succeeding Jurassic forms. The form of the limb elements was somewhat exaggerated in Baur's figures, and his suggestion concerning the origin of the outer element in the mesopodial region in the limb of *Baptanodon* is perhaps overstated, but his fundamental theory was correct. Baur set aside the Triassic ichthyosaurs with elongated epipodial elements separated by a cleft as a distinct genus, *Mixosaurus*, and divided the Ichthyosauria into three families; the MIXOSAURIDAE with elongated and separated epipodial bones and differentiated dentition; the ICHTHYOSAURIDAE with short epipodials which touch each other, and numerous teeth of nearly uniform shape; the BAPTANODONTIDAE with three epipodial elements, and no teeth.

In 1891 Fraas described and figured several jaw fragments, a humerus, and a number of vertebrae from the Wellendolomit of South Germany, referring all of these specimens to *Mixosaurus atavus* (Quenstedt). Attention was called to the contrast between the depressed crowns of the posterior teeth and the slender conical crowns of those farther forward in the jaw. The insertion of the teeth was also found to differ from that in *Ichthyosaurus*, inasmuch as the fangs were set into the jaw instead of resting in an open groove. The separate zygapophysial facets of the vertebrae were shown to be placed in intersecting planes, in contrast to the facets in *Ichthyosaurus*, where they are brought into the same plane and united medially. The vertebral centra were found to be deeply biconcave, and to be perforated by the chorda dorsalis in the caudal region. The specimens referred to *M. atavus* were divided into two varieties, *major* and *minor*.

In 1895 Merriam described the genus *Shastasaurus* from the Upper Triassic of northern California. The type specimen consisting of eight connected vertebrae, an arch bone and several ribs was distinguished from other genera by the thickened neural spines of the vertebrae, the single-headed dorsal ribs and the peculiar form of the coracoid. The element held to be a coracoid by the writer, and by all others who have expressed an opinion as to its character, was found later to be a pubis quite different from any known ichthyosaurian element. The vertebrae and ribs were from the posterior dorsal region.

In 1902 the description of the Californian Triassic ichthyosaurs was continued by Merriam with better material available. From these specimens it was possible to determine the principal characters of the skeleton, excepting the anterior portion of the skull and the phalangeal region of the paddles. The material was also found to represent several specific forms, one of which, *Shastasaurus perrini*, was later removed as a distinct genus, *Delphinosaurus*. In this publication Leidy's types of the Middle Triassic ichthyosaurs of Nevada were redescribed, and attention was called to their similarity to the shastasaurian forms. A collection of ichthyosaurian material obtained from the Middle Triassic of Nevada by the University of California before this paper appeared was referred to as apparently representing *Cymbospondylus petrinus* of Leidy. This material was stated to show a number of peculiar characters not recognized in specimens previously examined.

In November 1902 a fully illustrated paper by Repossi furnished the first definite information regarding the general skeletal structure of *Mixosaurus*. In Repossi's figures it was shown that *Mixosaurus* possessed many primitive characters that had not been recognized before. It appeared also to be much more closely related to the American Triassic forms than had been supposed. Also in 1902, there appeared Yakowlew's publication on a new find of ichthyosaurian remains from Spitzbergen, in which the large Spitzbergen form (*Ichthyosaurus polaris* of Hulke) was shown to have single-headed dorsal ribs, and was referred to *Shastasaurus*.

In von Huene's valuable work on the Triassic Reptilia, issued in 1902, there was given a brief review of the literature on the Ichthyosauria. Von Huene also presented the first figures of the interclavicle of a Triassic form, showing an interesting evolution from a deltoid Triassic type to the T-shaped element of the Jurassic ichthyosaurs. New material from the vertebral column was also described and figured.

In 1903 new material from California made possible the description of a complete anterior limb of an American Triassic ichthyosaurian. (Merriam, 1903, 1). In this genus (*Leptocheirus* Merriam—*Merriamia* Boulenger) instead of the primitive pentadactyl structure of the mixosaurian limb only three complete digits were represented. In another form, *Toretocnemus,* the hind limb was fully as large as the anterior one, but there were apparently only three digits and a very rudimentary fourth in the podial region. The pelvis of *Toretocnemus* was plate-like, and the pubis perforated by an obturator foramen. The middle dorsal vertebrae, unlike those of *Shastasaurus* and *Delphinosaurus,* supported double-headed ribs.

The first description of other than fragmentary remains from the Middle Triassic of America appeared in 1895 in the discussion of a finely preserved pectoral arch with the propodial and epipodial limb segments (Merriam, 1905, 2). The shoulder girdle of this form differed from that of any other known ichthyosaur, and the limb elements appeared to be the most primitive then known in the Ichthyosauria.

GEOLOGIC AND GEOGRAPHIC OCCURRENCE.

The geographic range of the Triassic ichthyosaurs is remarkably wide almost as far back as we can trace the group. Even from the Middle Triassic, remains are known from both Europe and western North America. From the Upper Triassic they are known from these regions, and possibly from others also.

Europe.—The oldest known remains of Ichthyosauria are those from the lower portion of the Muschelkalk of Germany and Switzerland. Fraas (1891, p. 37) states that the localities in the Swabian Muschelkalk at which specimens have been found represent a very constant horizon in the Wellendolomit. Unfortunately the material obtained consists only of isolated vertebrae, jaw fragments, or other separated parts of the skeleton. As yet no complete skeletons have been discovered.

A small amount of material from the lower Muschelkalk of southwest Germany and northern Switzerland is preserved in the collections of the Koeniglichen Naturalien-Cabinet, and in that of the Technische Hochschule in Stuttgart, in the Geologisch-Mineralogisches Institut in Tuebingen, and in the Polytechnikum in Zürich. A few specimens of ichthyosaurian vertebrae from the lower Muschelkalk in North Germany are preserved in the geological Museum of Halle a. S. Of the Swabian localities where material has been found in the Wellenkalk of the lower Muschelkalk, Fraas has mentioned Rhordorf, Calw, Aach, and Niederschach. The vertebrae at Zürich came from the Wellendolomit of Laufenberg in Canton Aargau and from Obereggingen. Material from the Wellenkalk of Querfurt north of the Harz is in the museum at Halle a. S.

From the middle of Muschelkalk of Freyburg a. U. ichthyosaur-like vertebrae have been obtained.

The upper Muschelkalk of Bayreuth has furnished several valuable specimens, including vertebrae and elements from both pectoral and pelvic arches.

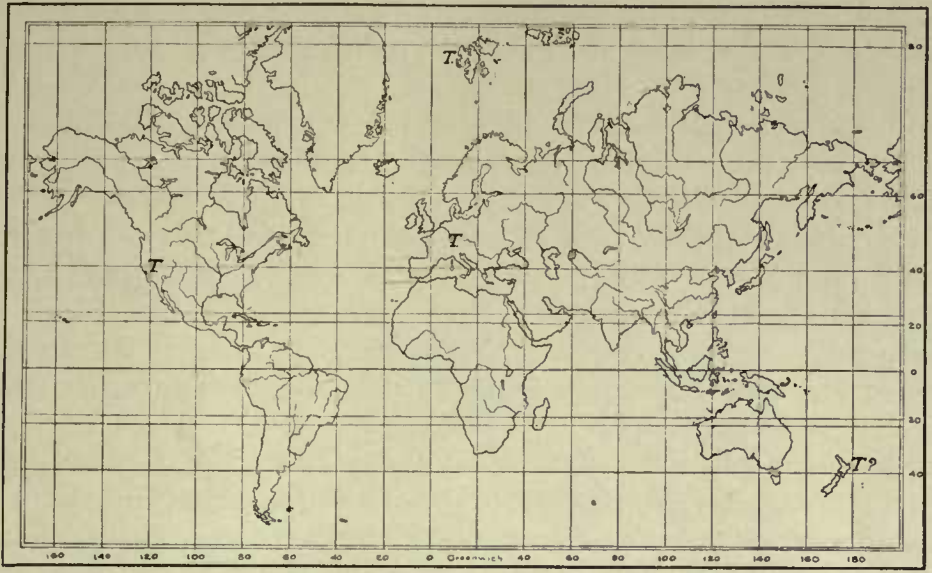

Fig. 1. Outline map of the world, on which the regions where Triassic ichthyosaurian remains have been found are marked with the letter *T*.

Descriptions of some of these specimens will probably appear in the near future. Also from the upper Muschelkalk are several vertebrae of ichthyosaurians from Grossreifling in Steiermark. From this locality there was also obtained in 1843 a very large skull with numerous vertebrae and other elements of the skeleton. This specimen was destroyed by fire in the museum of Admont in 1863. No careful study of it was made by a specialist in vertebrate palaeontology. At the present time there is some uncertainty as to its true character. H. von Myer (1847, pp. 190 and 191) described it from a sketch, and from information furnished by others, and compared it with *Ichthyosaurus platyodon*. A copy of an old sketch reproduced by von Arthaber (1896, p. 14) does not show any characters which indicate other than ichthyosaurian affinities. Other upper Muschelkalk remains, now in the mineralogical museum of Jena, are known from beds near Weimar.

Not until the Upper Triassic is reached in Europe do we find ichthyosaurian remains which give more than suggestions as to the true nature of the forms in the Triassic which they represent. The most abundant and important Triassic ichthyosaur material known in Europe is that from the bituminous shales of Besano in the vicinity of lake Lugano in northern Italy. This horizon has been stated to be the equivalent of the Raibl.[1] The Raibl is referred to the Upper Trias,[2] but more recent investigations have seemed to show that this horizon may be somewhat older. The material comprises a number of finely preserved skeletons exhibiting practically all parts of the skeletal structure. In addition there are a number of isolated parts of skeletons which help to interpret some of the larger specimens. On this material Bassani (1886) based *Ichthyosaurus cornalianus,* which later became the type of Baur's (1887) genus *Mixosaurus.*

From the Rhaetic portion of the Upper Trias Sauvage (1876) has described fragmentary remains apparently representing two species of primitive ichthyosaurs, *Ichthyosaurus rhaeticus* and *I.* (?) *carinatus.* Vertebrae are also known from the Swabian Bonebed (von Huene, 1902) and from the Koessner bed of Achnerthal (von Meyer, 1856). From Rhaetic beds near Bristol, England, a number of ichthyosaurian remains are also reported (Phillips, 1871).

Spitzbergen.—The occurrence of ichthyosaurian remains in the Triassic Spitzbergen was made known by Hulke in 1873 in a short paper on some fragmentary material obtained by a Nordenskiöld expedition in 1864 and 1868. The remains were referred to *Ichthyosaurus* by Hulke. Later observation by Merriam (1902) and Yakowlew (1902) have shown that Hulke's specimens were related to *Shastasaurus.* Dames (1895) supposed them to belong in *Mixosaurus,* but was unfortunately not well acquainted with the structure of that form, and also misinterpreted the first description of *Shastasaurus.* The original material of Hulke's species was lost after being studied by Dames in 1895.

A good fragment of a vertebra, obtained by the Russian-Swedish expedition in 1899-1901, was described by Yakowlew (1902) and referred to *Shastasaurus.*

New Zealand.—In 1874 Hector described from New Zealand an ichthyosaurian vertebra obtained in a micaceous sandstone in the Rangitata district of the province of Canterbury. The formation in which it occurred was said to be identical with other strata considered to be Triassic.

America.—The occurrences of Triassic ichthyosaurians in America have thus far been limited to exposures of the marine Trias in California and Nevada (fig. 2). As in Europe, remains are known from both the Upper and Middle Triassic, the oldest known specimens coming from the Middle Trias. The Upper, Middle and Lower Trias are all three represented in California and

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[1] Bassani, F., Atti Soc. Ital. Sc. Nat., vol. 29. Milano, 1886.

[2] See table on p. 16.

probably in Nevada also, but the conditions favoring the preservation of fossils are not similar in corresponding horizons of the two regions. For this reason it has chanced that ichthyosaurs are known as yet only from the middle division of the Trias in Nevada and from the upper division in California. In the fossiliferous marine Lower Triassic limestones of California and Idaho no remains of reptiles have yet been obtained, though marine fishes are common in the Lower Triassic of Idaho.

The geological correlation of the marine Triassic of the Pacific Coast region of America has been made the subject of careful investigation by Professor James Perrin Smith, from whose work on the stratigraphy of the West American marine Trias[3] the table on the following page has been extracted.

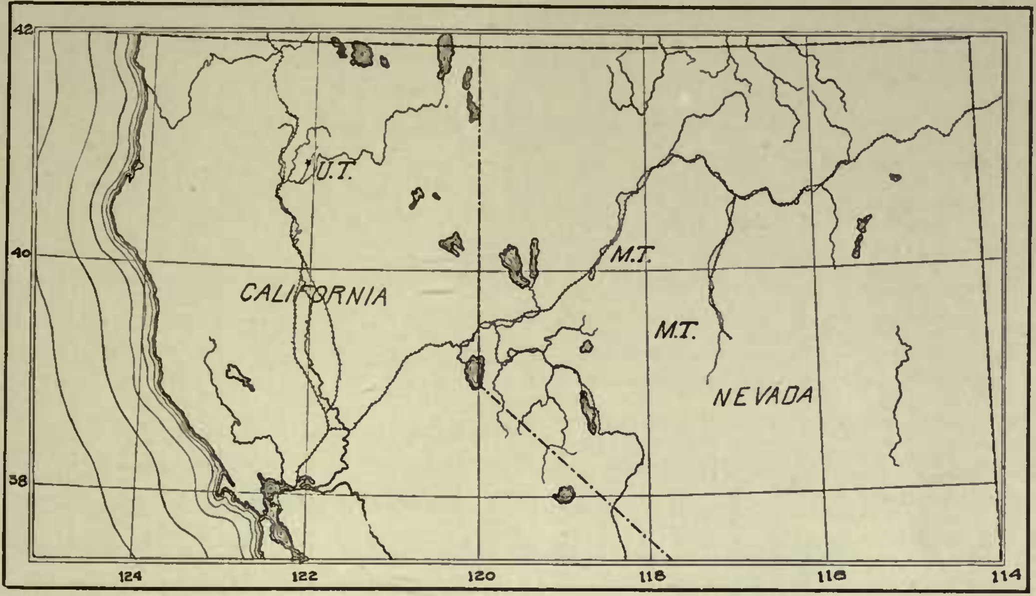

Fig. 2. Sketch map of northern California and northwestern Nevada, giving occurrence of Triassic formations in which ichthyosaurians have been obtained; *UT*, Upper Triassic; *MT*, Middle Triassic.

The *Upper Triassic* beds containing ichthyosaurian remains in California are largely exposed in Shasta County between the west side of Pit river and Squaw creek.[4] Large exposures form the imposing gray cliffs and peaks along the top of the prominent series of points known as Brock mountain (pl. 1, fig. 2). The outcrops also cross Pit river to the south, and extend to the north in rather narrow exposures beyond the headwaters of the North Fork of Squaw creek. The formation consists principally of the phase known as the Hosselkus Limestone. It is rather sharply divided lithologically into an upper and a

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[3] Smith, Jas. Perrin, Festschrift zum siebzigsten Geburtstage von Adolf v. Koenen, 1907.

[4] Diller, J. S., U. S. Geol. Surv., Redding folio.

INTERREGIONAL CORRELATION OF THE TRIAS (ADAPTED FROM JAS. PERRIN SMITH)

<table>
<tr><th></th><th colspan="3">Mediterranean region</th><th colspan="3">Arctic-Pacific region</th><th colspan="7">American region</th></tr>
<tr><th></th><th>German</th><th colspan="2">Alpine</th><th colspan="3"></th><th colspan="2">California</th><th colspan="2">Nevada</th><th colspan="2">Idaho</th><th>Brit. Col.</th></tr>
<tr><td rowspan="7">UPPER TRIAS</td><td>Rhaet</td><td colspan="2"></td><td colspan="3"></td><td colspan="2"></td><td colspan="2"></td><td colspan="2" rowspan="10"></td><td></td></tr>
<tr><td rowspan="6">Keuper</td><td rowspan="2">Noric limestone of Hallstatt</td><td rowspan="2"><i>Pseudomonotis ochotica</i> in the Crimea</td><td colspan="3" rowspan="2"><i>Pseudomonotis ochotica</i> slates of northern Sibera, Japan and Indian Ocean</td><td colspan="2"><i>Pseudomonotis subcircularis</i> slates with <i>Rhabdoceras</i> and <i>Halorites</i></td><td colspan="2"><i>Pseudomonotis</i> slates with <i>Rhabdoceras</i> and <i>Placites</i></td><td><i>Pseudomonotis</i> slates</td></tr>
<tr><td rowspan="4">Hosselkus limestone</td><td><i>Spiriferina</i> beds</td><td colspan="2" rowspan="5">Star Peak limestones without characteristic fossils</td><td></td></tr>
<tr><td colspan="2">Sandling beds with <i>Tropites subbullatus</i></td><td colspan="3"></td><td><i>Juvavites</i> beds
Beds with <i>Tropites subbullatus</i></td><td rowspan="3"><i>Dawsonites</i> beds</td></tr>
<tr><td colspan="2">Raibl beds with <i>Trachyceras aonides</i></td><td colspan="3" rowspan="3"><i>Dawsonites</i> slates of Bear Island</td><td><i>Halobia superba</i> beds</td></tr>
<tr><td colspan="2">Cassian beds with <i>Trachyceras Aon</i></td><td>Slates with <i>Halobia</i> conf. <i>rugosa</i></td></tr>
<tr><td colspan="2">Wengen beds with <i>Trachyceras Archelaus</i></td><td rowspan="4">Pit Formation</td><td rowspan="2">Slates and tuffs without determinable fossils</td><td rowspan="2"><i>Daonella</i> beds</td></tr>
<tr><td rowspan="4">MIDDLE TRIAS</td><td>Upper Muschelkalk</td><td colspan="2">Buchenstein beds with <i>Trachyceras Reitzii</i></td><td colspan="3">Ceratite slates of Japan with <i>Anolcites</i> and <i>Danubites</i></td><td rowspan="3"><i>Daonella</i> limestones in western Humboldt Range</td><td rowspan="3"><i>Daonella dubia</i> beds with <i>Ceratites trinodosus</i></td></tr>
<tr><td>Middle Muschelkalk</td><td>Reifling limestone</td><td>Limestones of Han Bulog, Bakony and the Schrey Alps with <i>Ceratites trinodosus</i></td><td rowspan="3">Beds of Ussuri Bay in eastern Siberia with <i>Monophyllites sichoticas</i></td><td rowspan="3">Mengilaeh beds?</td><td><i>Daonella</i> limestones of Spitzbergen</td><td rowspan="2">Clay- and silicious slates with <i>Anolcites</i> conf. <i>Whitneyi</i> and <i>Ceratites</i> conf. <i>humboldtensis</i></td><td rowspan="6"></td></tr>
<tr><td rowspan="2">Lower Muschelkalk with <i>Hungarites Strombecki</i></td><td colspan="2"><i>Ceratites binodosus</i> beds in the South Alps</td><td rowspan="2"><i>Posidonomya</i> limestones of Spitzbergen</td></tr>
<tr><td colspan="2">Beds at Gulf of Ismid in Asia Minor</td><td rowspan="3">Ceratite limestones of Inyo Range</td><td>Black limestones with <i>Parapopanoceras</i>, <i>Xenodiscus</i>, <i>Acrochordiceras</i>, and <i>Hungarites</i></td><td colspan="2" rowspan="4"></td><td rowspan="4">Aspen beds</td><td></td></tr>
<tr><td rowspan="3">LOWER TRIAS</td><td rowspan="3">Buntsandstein</td><td rowspan="3">Werfen beds</td><td>Campil beds with <i>Tirolites cassianus</i></td><td colspan="3">Olenek beds of northern Siberia</td><td>Calcareous slates without fossils</td><td><i>Columbites</i> beds
<i>Tirolites</i> beds</td></tr>
<tr><td>Seis beds with <i>Pseudomonotis Clarai</i></td><td colspan="3"><i>Proptychites</i> beds of Ussuri Bay in northern Siberia</td><td><i>Meekoceras</i> beds of Inyo County, California with <i>Meekoceras gracilitatis</i>, <i>Ussuria</i>, <i>Pseudosageceras</i>, <i>Inyoites</i>, <i>Owenites</i>, <i>Nannites</i></td><td><i>Meekoceras</i> beds</td></tr>
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lower portion (pl. 1, figs. 2 and 3). The upper part consists of very massive, gray limestones. The lower beds are composed of dark gray or black, somewhat shaly limestones, and bands of calcareous black shales. Below the lower division are the black Pit Shales of the Middle Trias.

The Hosselkus Limestone contains in its fauna a large number of invertebrate forms, of which the greater number of the species are Cephalopoda. In addition to the Ichthyosauria, the vertebrates are represented by the thalattosaurian reptiles, and by a few fishes.[5] A list of the characteristic species would include the following:

Tropites subbullatus Hauer.
Tropites dilleri Smith.
Discotropites sandlingensis Hauer.
Sagenites herbichi Mojsisovics.
Juvavites subintermittens Hyatt and Smith.
Polycyclus henseli Oppel.
Arpadites gabbi Hyatt and Smith.
Californites merriami Hyatt and Smith.
Clionites compressus Hyatt and Smith.
Sandlingites andersoni Hyatt and Smith.
Sirenites lawsoni Hyatt and Smith.
Trachyceras lecontei Hyatt and Smith.
Hauerites ashleyi Hyatt and Smith.
Arcestes pacificus Hyatt and Smith.
Cosmonautilus dilleri Hyatt and Smith.
Orthoceras shastense Hyatt and Smith.
Halobia superba Mojsisovics.
Terebratula, sp. indet.
Rhynchonella, sp. indet.
Myophoria, sp. indet.
Thalattosaurus alexandrae Merriam.
Thalattosaurus perrini Merriam.
Nectosaurus halius Merriam.
Hybodus shastensis Wemple.
Acrodus wempliae Jordan.

Ichthyosaurian remains have been found in nearly all horizons of the Hosselkus Limestone. They are nowhere very abundant, several years work having brought in only about twenty good specimens. They are most numerous in the *Tropites subbullatus,* and *Juvavites* horizons near the top of the lower division. In the lower, more shaly beds little material has been found, but the specimens occurring there were in good state of preservation and the elements were not badly scattered. In a well-marked bed a short distance below the top of the lower division many loose vertebrae and other skeletal elements have been found associated with comminuted shells, evidently representing somewhat shallower water than the rest of the deposits. In the massive, gray beds of the upper Hosselkus Limestone the remains are usually fragmentary and scattered. Some large specimens showing connected parts of skeletons have, however, been found there.

As yet the genera *Delphinosaurus, Toretocnemus* and *Merriamia* are known only from the beds some distance below the top of the lower division, *Shastasaurus* occurs in both lower and upper divisions, but is represented in the upper beds principally by the gigantic *S. careyi.*

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[5] Merriam, J. C., The Thalattosauria. Mem. Calif. Acad. Sci., vol. 5, no. 1.
Wemple, Miss E. M., New Cestraciont Teeth from the West-American Trias., Univ. Calif. Publ. Geol., vol. 5, no. 4.
Jordan, D. S., The Fossil Fishes of California, Univ. Calif. Publ., vol. 5, no. 7.

In the Upper Triassic specimens, excepting in a very few instances, the limestone matrix is cemented to the bones, making the work of preparation more than ordinarily difficult. In the case of small specimens, etching with hydrochloric acid has been found advantageous; the blue tint of the mineral viviante appearing in the bones, making their outlines comparatively distinct.

The *Middle Triassic* ichthyosaurs of the Pacific Coast region have thus far been known only from the limestones of the West Humboldt and New Pass ranges of Western and Central Nevada (fig. 2). Search has been made in the Middle Triassic shales of California but without any definite results.

The most important occurrences are those in the exposures along the eastern side of the West Humboldt Range. Wherever the limestones are exposed bones may occur. The most important finds have been made at Cottonwood, Buena Vista, Straight, Indian, American, and Fisher cañons. In the south fork of American Cañon on the two points known as Saurian Hill and Fossil Hill (pl. 1, fig. 1) skeletons were particularly numerous and well preserved.

The horizon at which the ichthyosaurs of the West Humboldt Range occur is apparently a constant one, representing the middle portion of the Middle Triassic. The associated invertebrate fauna as described by James Perrin Smith includes with others the following characteristic forms:

Daonella dubia Gabb.
Orthoceras dubium Gabb.
Atractites conf. *crassirostris* Hauer.
Ceratites trinodosus Mojsisovics.
Anolcites americanus Mojsisovics.
Acrochordiceras hyatti Meek.
Gymnites aff. *bosnensis* Hauer.
Ptychites meeki Hyatt and Smith.
Celtites halli Mojsisovics.
Monophyllites billingsianus Gabb.
Sageceras gabbi Mojsisovics.
Eutomoceras dunni Smith.
Joannites gabbi Meek.
Beyrichites rotelliformis Meek.

This fauna is that of the characteristic *Ceratites trinodosus* horizon, and *C. trinodosus* is a common species.

In addition to the Ichthyosauria there have been found in these beds a few fishes, and some reptilian forms which are as yet only imperfectly known. The following are the described forms.[6]

Acrodus alexandrae Wemple.
Acrodus oredontus Wemple.
Hybodus nevadensis Wemple.
Omphalosaurus nevadanus Merriam.

The skeletons are in general better preserved in the Middle Triassic beds of Nevada than in the later limestones of northern California, and are more easily freed from the matrix. The limestone is often slightly shaly, and is frequently separated from the bone by a thin film of argillaceous material heavily impreg-

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[6] Wemple, Miss E. M., New Cestraciont Teeth from the West-American Trias. Univ. Calif. Publ. Geol., vol. 5, no. 4.

Merriam, J. C., Preliminary Note on a New Marine Reptile from the Middle Triassic of Nevada. Univ. Calif. Publ. Geol., vol. 5, no. 5.

nated with iron oxide. In a few localities of comparatively small area the ichthyosaur skeletons are very numerous. The writer is not aware of any locality in other formations at which remains of ichthyosaurs are more abundant.

At American Cañon, where the most extensive work has been carried on, the beds have fortunately been repeated twice by faults, giving a large exposure of the most fossiliferous strata. In this region, between thirty and forty good specimens were obtained on Saurian Hill, and from the same bed repeated on Fossil Hill farther to the east.

In many cases there seems to be a concretionary formation about the skeletons. This is mostly distinctly shown in the case of the skull, which may be enclosed in a rounded nodular mass. This structure is noticeable also in following the vertebral column, the layer containing the vertebrae often pinching out on both sides of the skeleton. Unfortunately the ends of the limbs seem often to have extended beyond the nodular envelope, and are not to be found in the rock immediately outside of it.

The Triassic beds in the New Pass Range are of nearly the same age as those in the West Humboldt Range. The exosures are not as extensive as in the West Humboldt Range and the beds are hardly as rich in fossils.

The following are, according to Professor Smith, the most characteristic species of this locality:

Celtites neumari Mojsisovics.
Ceratites (Paraceratites) trinodosus Mojsisovics.
Trachyceras americanum Meek.
Ceucoceras bonae-vistae Hyatt and Smith.
Arcestes gabbi Meek.
Gymnotoceras blakei Gabb.

In the New Pass Range thirty miles west of Austin and three miles west of the New Pass mine several parts of ichthyosaurian skeletons were obtained. The first specimen of a Middle Triassic ichthyosaurian to be described from America was found at this locality (Leidy, 1868).

The Middle Triassic limestones are represented at other points in Nevada, and will probably be found to have ichthyosaurian remains more or less abundantly represented in them wherever they occur.

Though it is probable that the Ichthyosauria had become marine forms as early as Lower Triassic time, no one has yet succeeded in obtaining in America any material representing the group from beds lower than the middle division of the Trias. The marine Lower Trias of eastern California and particularly of southeastern Idaho is very rich in fossils, including cephalapods, with which ichthyosaurs are elsewhere associated; but as yet no bones have been obtained which can be referred to reptilian orders. Bones of crossopterygian fishes are fairly common in these beds[7] in association with cephalapods.

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[7] Goddard, M., Fish Remains from the Marine Lower Triassic of Aspen Ridge, Idaho. Univ. Calif. Publ. Geol., vol. 5, no. 8. Also, Evans, H. M., A New Cestraciont Spine from the Lower Triassic of Idaho. Univ. Calif. Publ. Geol., vol. 3, no. 18.

The distribution of the Triassic ichthyosaurs, ranging as it does from Europe and Spitzbergen to western North America and possibly to New Zealand, apparently indicates that these forms were in existence as a marine type for a considerable period even antecedent to Middle Triassic time. As early as the Middle Triassic, forms showing a considerable degree of specialization were present in western Europe and in western North America. Even though a wide range of open sea between these two provinces be presumed to have existed, such a wide distribution as is seen here could not have been accomplished in less than a considerable part of an epoch.

The wide distribution of the Ichthyosauria in Middle Triassic time with the absence of any known remains from the Lower Triassic makes it difficult to determine even approximately the place of origin of the group.

GENERAL SKELETAL STRUCTURE OF THE TRIASSIC ICHTHYOSAURS.

Though there is much variation in the structure of the ichthyosaurians known from the Triassic, and there is good reason for considering them as divisible into several natural subgroups, it is also true that they are evidently a unit or a distinct group, the greater part of the evolution or differentiation of which from the primitive type has taken place in Triassic time. It has therefore seemed important for purposes of comparison to consider the general structure of all the known forms together. In another portion of this paper the characteristics of the subgroups are discussed separately.

Skull.

In all Ichthyosauria, whether from the Triassic or from later periods, there is a remarkable similarity of general characters in the structure of the skull. Though considerable differences appear in a comparison of all the known forms, particularly in contrasting the oldest genera with the most recent ones, these differences consist in the main of variations in the proportions of parts, and almost no radical changes of characters such as may occur in other parts of the skeleton are found here. The modifications or variations which present themselves during the known history of the group are in the main closely related to variations in the length of the elements of the facial region, or to change in the size of the orbits. The varying characters seem to be almost entirely of the adaptive type, and indicate a close relationship between the evolutionary changes in the group and the greatest needs of the animal under the particular conditions obtaining in its habitat.

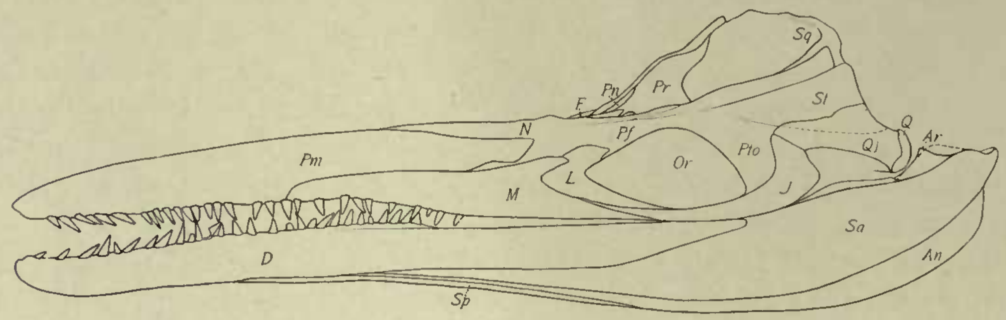
The structure of the skull is well shown in the Italian mixosaurs, but as yet no detailed study of this portion of the skeleton has been carried out in these specimens, and only the most general observations can be made on the figures available. Of the other material obtained in Europe, only a few fragments are known. Of the American Upper Triassic fauna the skulls of *Shastasaurus, Merriamia* and *Delphinosaurus* are known in part, but without satisfactorily showing the features which ordinarily give most definite expression to variation tendencies. Of the American Middle Triassic *Cymbospondylus* practically the entire skull structure is well shown in several excellent specimens (pls. 2 to 6). As *Cymbospondylus* is the only Triassic genus of which the skull is well known, its description is made the basis for the following discussion of the skull of the Triassic Ichthyosauria in general.

Although it represents one of the most ancient known ichthyosaurs and is relatively primitive in many respects, the skull of *Cymbospondylus* is still typically ichthyosaurian. While its structure, like that of the limbs, approximates that of shore types more closely than do the corresponding features in the Jurassic ichthyosaurs, it is as a whole, surprisingly specialized, and is evidently the product of an ancestry which had expressed this special type of aquatic adaptation for a long period. Like the typical Jurassic genera, the facial region is relatively long and slender, the premaxillaries and nasals are very largely developed, the frontals are small or are largely covered by the nasals, the superior nares occupy a nearly median position, and a heavy sclerotic ring is present. On the other hand in the relatively greater size of the maxillaries, smaller orbits, and broader temporal bar, the skull is more primitive than any described form from a later period.

The skull as a whole is relatively short compared with the length of the trunk. As nearly as can be estimated its length equals little more than one-third that of the dorsal region. The skull of *Mixosaurus* seems to be relatively much longer, equalling about two-thirds the length of the trunk, while in *Ichthyosaurus* its relative length may be as great as 80 per cent.

Facial Region.—The antorbital portion of the skull (fig. 3) is elongated and narrow as in the typical Ichthyosauria. It is, however, shorter relative to the total length of the skull, than in any other ichthyosaurian known to the writer, excepting the short-faced *Ichthyosaurus breviceps* from the Lower Lias of England. In *Cymbospondylus* (no. 9950) it equals about 60 per cent. of the total length of the skull, and in *I. breviceps* 55 per cent. At the same time the extent of the maxillary anterior to the orbit is relatively larger than in any other ichthyosaurian. It amounts to 48 per cent. of the length of the antorbital region in specimen 9950, while in *I. breviceps* with a somewhat shorter rostrum, in which one would expect to find the maxillary relatively long, it is less than 40 per cent. In *Mixosaurus* the length relative to the cranial region is a little less than in *Cymbospondylus.*

The *premaxillaries* are greatly elongated, extending more than half the total length of the skull. For a little more than half of their length measured back from the anterior end of the rostrum they are united dorsally. Behind the region of contact with each other they are separated by the nasals.



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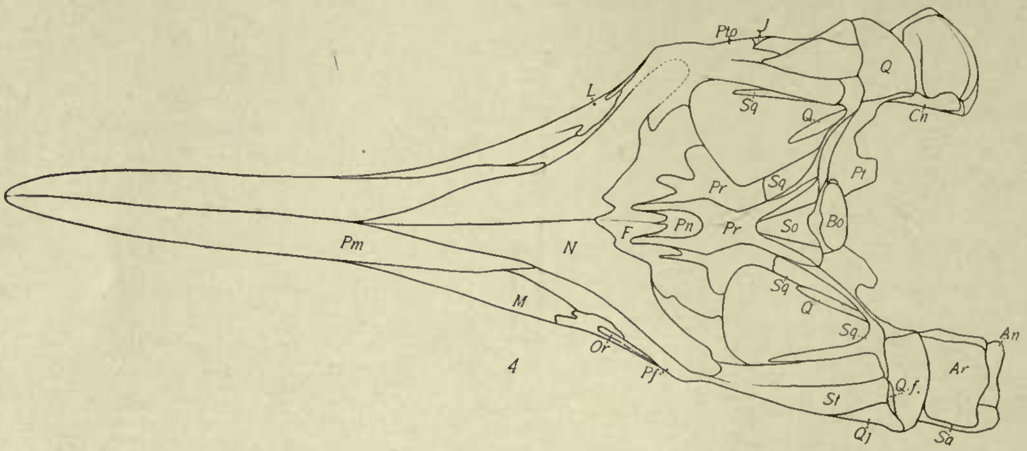

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Figs. 3 and 4. *Cymbospondylus petrinus* Leidy. Skull × ⅙. Fig. 3, side view; fig. 4, superior view. *Pm*, premaxillary; *M*, maxillary; *N*, nasal; *L*, lachrymal; *J*, jugal; *Or*, orbit; *F*, frontal; *Pf*, pre- and post-frontal; *Pto*, postorbital; *Pr*, parietal; *Pn*, pineal foramen; *Sq*, squamosal; *St*, supratemporal; *Q*, quadrate; *Qj*, quadratojugal; *Q.f.*, quadrate foramen; *Pt*, pterygoid; *So*, supraoccipital; *Bo*, basioccipital; *Ar*, articular; *An*, angular; *Sa*, surangular; *Cn*, coronoid; *Sp*, splenial; *D*, dentary.

The *maxillaries* are longer than in any other described ichthyosaurian, both in relation to the length of the rostral region and to that of the cranium; and almost, if not quite, half of the dentigerous margin of the upper jaw is situated on these elements. In *Mixosaurus* the length of the maxillaries is also relatively great.

The *superior nares* are situated much as in *Ichthyosaurus,* though apparently occupying a slightly more advanced position than in most forms.

The *nasals* (fig. 4) are large and extend back over the frontals as in other Ichthyosauria. They are relatively very widely expanded, much as in *Ichthyosaurus* and *Baptanodon*. No comparison with *Mixosaurus* has been made, as the writer has not been able to make certain of the form of this element in that genus. From Repossi's figures of the skull (Repossi, 1902, tav. 9, fig. 1) one suspects that the nasals are very large.

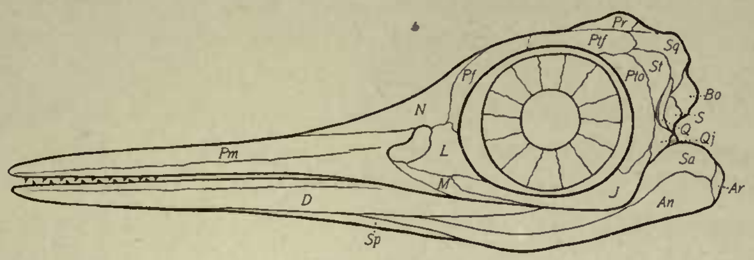

Fig. 5. *Opthalmosaurus icenicus* Seeley. Skull. (Adapted from C. W. Andrews.) About ⅙ natural size. *Pm*, premaxillary; *M*, maxillary; *N*, nasal; *L*, lachrymal; *J*, jugal; *Pf*, prefrontal; *Ptf*, postfrontal; *Pto*, postorbital; *Pr*, parietal; *Sq*, squamosal; *St*, supratemporal; *Qj*, quadratojugal; *Q*, quadrate; *S*, stapes; *Bo*, basioccipital; *Ar*, articular; *Sa*, surangular; *An*, angular; *Sp*, splenial; *D*, dentary.

Fronto-Parietal Region.—As in *Ichthyosaurus* the anterior portion of the cranial region is covered by the expanded nasals. A little more of the frontal element seems to be exposed than often occurs in *Ichthyosaurus*. The large pineal foramen is surrounded mainly by the parietals, instead of wholly or to a large extent by the frontals as in *Ichthyosaurus*.

Orbital Region.—One of the most striking features of the skull in *Cymbospondylus* is the relatively small size of the orbit, compared with the orbital region of most species of *Ichthyosaurus*, or more particularly with *Opthalmosaurus* (fig. 5). Even in specimens crushed laterally so that the height of the orbit would tend to be increased, the relative size is practically the same as in the figure above (fig. 3). (See also pl. 6.) In *Baptanodon* as figured by Gilmore[8] the length of the orbit is only a little less than one-fourth that of the whole skull, including the much elongated snout. In *Cymbospondylus* it is about one-sixth the length, in spite of the fact that the rostral region is relatively short. The relative size of the orbit is particularly noticeable in comparison with the anteroposterior diameter of the temporal bar immediately behind it. The anteroposterior diameter of the temporal bar equals about 38 per cent. of the anteroposterior diameter of the orbit in *Cymbospondylus* (no. 9950); in *Baptanodon* it appears to be less than 25 per cent. Of the undistorted *Ichthyosaurus* skulls of which the writer is able to obtain any information, the forms which most nearly approach *Cymbospondylus* in these characters are *I. platyodon* and *I. lonchiodon* of the English Lower Lias.

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[8] Gilmore, C. W., Mem. Carneg. Mus., vol. 2, pl. 7.

In *Mixosaurus* and *Shastasaurus* the orbits are relatively large, though perhaps somewhat smaller than in *Ichthyosaurus*.

The sclerotic ring of *Cymbospondylus* (pl. 5, fig. 2) has much the same structure as in *Ichthyosaurus* and *Baptanodon*. The number of plates is about sixteen to eighteen. In *Ichthyosaurus* the number ranges from fifteen to twenty. Gilmore finds but fourteen plates in *Baptanodon*, and the same number is given for *Opthalmosaurus* by Andrews. The inner or median ends of the plates bend quite sharply over the equatorial region of the eyeball and extend for some distance over the inner side of the eye. The lateral flattening of the eyeball shown by the sharp curvature of the plates on the equator of the eye has been noted also for *Ichthyosaurus* by Owen[9] and recently on *Baptanodon* by Gilmore.[10] The relative size of the sclerotic ring agrees with that of the orbit in being smaller than in any of the later ichthyosaurs. The ring in *Ichthyosaurus platyodon* and in the short-headed *I. breviceps* is nearly half again as large as in *Cymbospondylus*.

Temporal Region.—The lateral temporal bar of *Cymbospondylus* is characterized by uncommon length anteroposteriorly. Its height is somewhat less than in most ichthyosaurs. Relative to the length of the cranial region it is much less elevated than in *Baptanodon*. Behind the jugal the inferior side of the temporal bar is sharply cut out so as to form with the slightly concave coronoid region of the mandible an elliptical opening with its long diameter extended anteroposteriorly. According to the suggestion of McGregor[11] the temporal bar originally contained a lateral temporal opening, which was closed through gradual anteroposterior compression of the bar owing to the enlargement of the orbit. In *Cymbospondylus* the bar shows fully as much area on the side of the skull as in many reptilian forms possessing a lateral temporal fenestra. As the quadratojugal passes above the inferior notch in the bar, it is improbable that this opening corresponds to a lateral temporal fenestra which was being lost in *Cymbospondylus* through breaking down of an inferior temporal arcade. Though there is no doubt that the temporal bar has been progressively reduced, it seems very doubtful whether it ever enclosed a lower or lateral temporal fenestra.

Occipital Region.—The occipital region of *Cymbospondylus* (fig. 6) seems to be well enclosed with bone and the posterior temporal openings are small. The basioccipital differs from that of other ichthyosaurians in presenting a strongly concave articular face for contact with the convex anterior face of the atlas. The inferior side of the basioccipital is characterized by the development of prominent hypapophyses similar to those of *Sphenodon*. The form of the lat-

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[9] Owen, R., Fossil Rept. Lias Form., pt. 3 (Monog. Pal. Soc., Lond., 1881), p. 103.

[10] Gilmore, C. W., Mem. Carneg. Mus., vol. 2, p. 328.

[11] McGregor, J. H., Mem. Amer. Mus. Nat. Hist., vol. 9, p. 91.

eral occipitals is not well known, but they seem to be perforated by large lateral foramina. The supraoccipital extends forward a considerable distance to form a part of the floor of a deep fossa between the posterior arms of the parietals. The form of the opisthotic and prootic are not certainly known. The stapes is not certainly recognized. If represented by an element which lies between the otic region and the quadrate (fig. 6, *x*) it is much smaller and more slender than in the later ichthyosaurs. It may also be noted that no distinct pit for the reception of the distal end of the stapes is visible on the inner side of the quadrate.

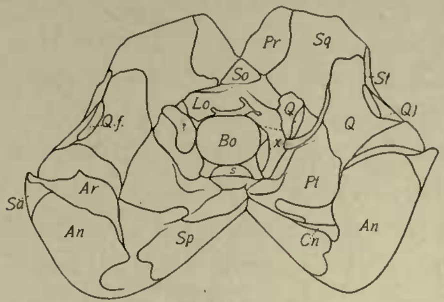

Fig. 6. *Cymbospondylus petrinus* Leidy. Skull, posterior view, × ⅙. *Pr*, parietal; *Sq*, squamosal; *St*, supratemporal; *Qj*, quadratojugal; *Q*, quadrate; *Q.f*, quadrate foramen; *So*, supraoccipital; *Lo*, lateral occipital; *Bo*, basioccipital; *S*, basisphenoid; *X*, stapes?; *Pt*, pterygoid; *Ar*, articular; *Sa*, surangular; *An*, angular; *Cn*, coronoid; *Sp*, splenial.

Quadrate and Suspensorium.—The quadrate is large and heavy and seems to be closely and broadly united with the adjoining elements, making the posterior angles of the skull particularly firm. The anterior side of the quadrate overlapping the pterygoid extends forward as a broad plate resembling that seen in the Rhynchocephalia. The face articulating with the mandible is crossed obliquely by a marked depression situated between two strongly convex faces. This form of the articular face on the quadrate has recently been noted also in *Ichthyosaurus platydactylus* by Broili,[12] and is suggested in *Sphenodon.*

The large quadrate foramina perforating the posterior angles of the skull

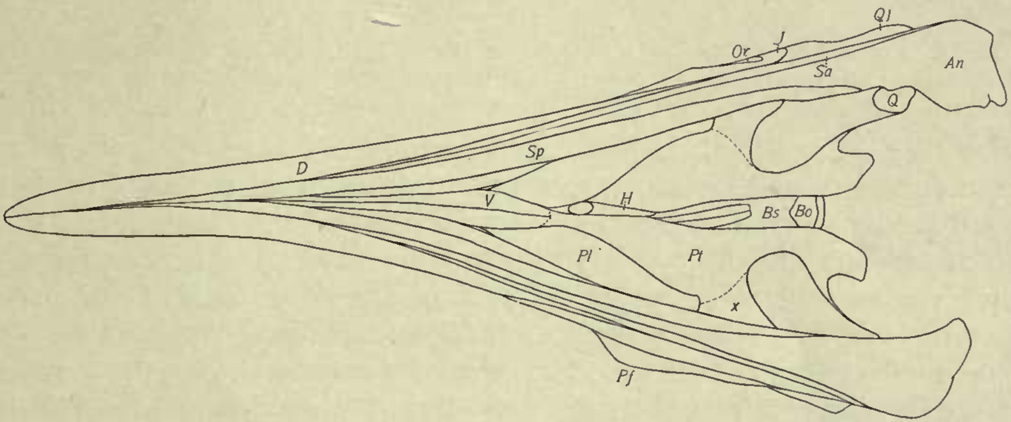

Fig. 7. *Cymbospondylus petrinus* Leidy. Skull, inferior view, × ⅙. *D*, dentary; *Sp*, splenial; *Sa*, surangular; *An*, angular; *Or*, orbit; *J*, jugal; *Qj*, quadratojugal; *Q*, quadrate; *Bo*, basioccipital; *Bs*, basisphenoid; *Pt*, pterygoid; *X*, ectopterygoid?; *H*, hyoid; *Pl*, palatine; *V*, prevomer?

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[12] Broili, F., Paleontg., Bd. 54, p. 140.

are situated much as in the later ichthyosaurs. The quadratojugal forming the outer boundary of the quadrate foramen is overlapped superiorly by the supratemporal. The inferior border of the quadratojugal extends forward and above the inferior temporal notch to meet the jugal.

Palatine Region.—The palate of *Cymbospondylus* (fig. 7) closely resembles that of *Ichthyosaurus* in most details of its structure. The roof of the mouth is largely covered by the expanded palatines and pterygoids, the median margins of the pterygoids approaching each other closely for a considerable distance back toward the basisphenoid. The pterygoids are characterized by prominent posterior projections of the median edges, which extend some distance back of the basioccipital. In specimen 9950 the posterior portion of the lateral wing on each of the pterygoids is separated from the main body of the bone in such a manner as to suggest that it represents a distinct element (fig. 7, *x*). If there is a separate bone here it is evidently a discrete ectopterygoid which has united with the pterygoid in all later forms.

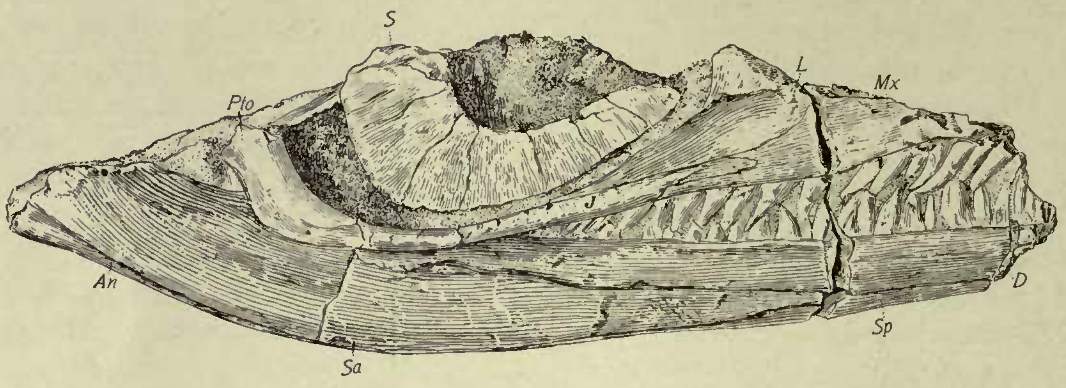


Fig. 8. *Merriami zitteli* (Merriam). Skull, lateral view, × 7/10. *An*, angular; *Sa*, surangular; *Sp*, splenial; *D*, dentary; *Mx*, maxillary; *L*, lachrymal; *J*, jugal; *Pto*, postorbital; *S*, sclerotic ring.

Mandible.—The lower jaw of *Cymbospondylus* is formed much as in the later ichthyosaurian genera, the relations of the several elements as they appear on the outer side of the rami being much as in *Ichthyosaurus.* In the genus *Merriamia* (fig. 8) possibly also in *Mixosaurus,* the surangular is relatively large and forms the principal part of the outer side of the posterior half of the jaw. In *Cymbospondylus* it forms the anterior side of the cotylus for the quadrate, and is thickened transversely anterior to the cup. As in the other ichthyosaurian genera there is no coronoid elevation, but the surangular presents a broad flat superior surface in the region of the coronoid. Below the coronoid margin there is, as in *Baptanodon,* a relatively small lamellar bone extending back almost to the posterior extremity of the inner side of the jaw (fig. 9), and representing the coronoid or the prearticular. The articular ex-

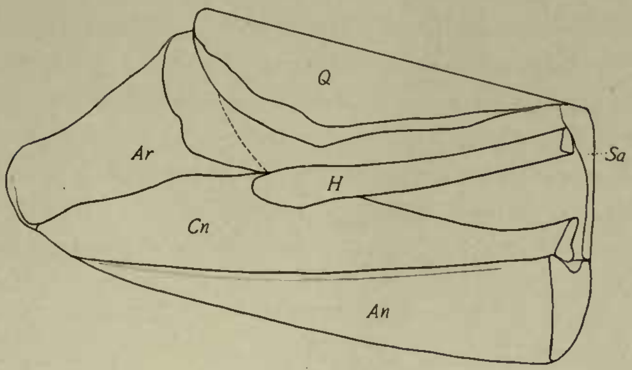
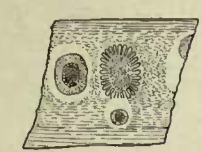


Fig. 9. *Cymbospondylus petrinus* Leidy. Inner side, posterior end of left ramus of mandible, × ⅓. *Ar*, articular; *Cn*, coronoid; *An*, angular; *Sa*, surangular; *H*, hyoid; *Q*, quadrate.

tends from the cotylus to the posterior end of the mandible. It is much thickened immediately behind the cotylus, and is thickened also at the posterior end. Between these regions the upper surface is strongly hollowed.

DENTITION.

In the specimens of *Cymbospondylus* that have been examined thus far the dentition has not been materially different from that of *Ichthyosaurus* excepting in the insertion of the teeth (figs. 10 to 12). The numerous teeth are all



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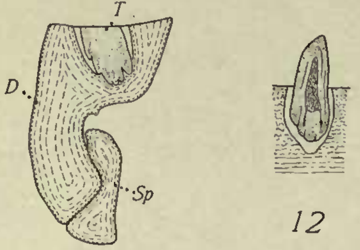

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Fig. 10. *Cymbospondylus petrinus* Leidy. Horizontal cross-section of dentary about 5 mm. below upper margin, showing teeth set in completely surrounded bone sockets, × ½.

Figs. 11 and 12. *Cymbospondylus petrinus* Leidy. Fig. 11, transverse cross-section of lower jaw showing teeth set in sockets in the dentary. Superior margin cut down several millimeters. *T*, tooth; *D*, dentary; *Sp*, splenial, × ½; fig. 12, anteroposterior cross-section of the base of a tooth set in the dentary, × ½.

simple conical, and are, in some cases at least, set in distinct pits. The base of the dentine cone is strongly folded (fig. 10), and there does not appear to be any considerable amount of cement covering it. As nearly as can be determined there were thirty to thirty-five, or more, teeth in each ramus of the jaws. Between the anterior and posterior ends of the jaws there is a slight difference in form, the posterior teeth being somewhat shorter and heavier (fig. 3). This is also true of the genus *Merriamia* (fig. 8), of which the dentition of the posterior half of the jaws is known. In *Merriamia* and in *Shastasaurus* the teeth, as far as known, are set in open grooves. Imperfect alveoli may, however, have been present in some of the regions of the jaw which have not yet been examined.

The characters seen in the American Triassic forms are in strong contrast to the nature of the dentition of *Mixosaurus* (figs. 13 and 14), in which the teeth show marked differentiation and are set in rather widely spaced distinct pits.

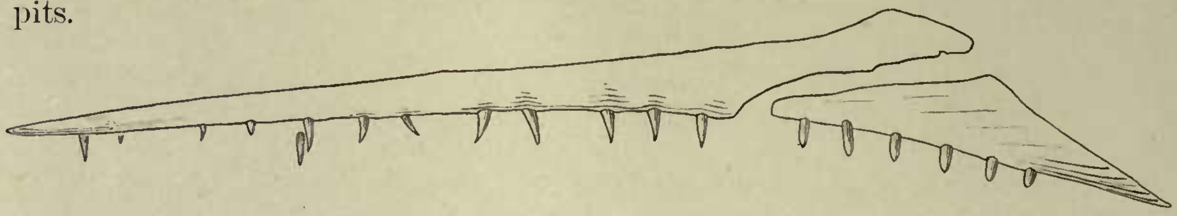

Fig. 13. *Mixosaurus cornalianus* (Bassani). Upper jaw and dentition, natural size. (Adapted from Repossi.)

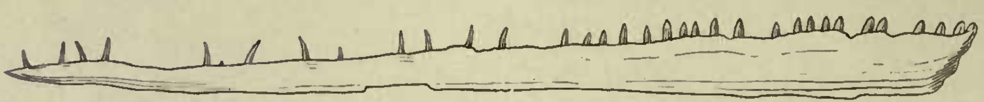

Fig. 14. *Mixosaurus cornalianus* (Bassani). Lower jaw and dentition, natural size. (Adapted from Repossi.)

As has been shown by Fraas (1891, p. 38) the dentition of *Mixosaurus* (?) *atavus* (figs. 15 and 16) is characterized by extreme differentiation of the teeth, by their firm insertion in slightly separated alveoli, by the coarse folds of the basal portion of the dentine cone, and by the extreme reduction of the cement.

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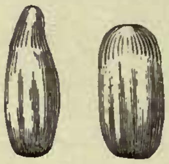

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Fig. 15. *Mixosaurus* (?) *atavus* (Quenstedt). Anterior end of lower jaw with dentition, natural size. (After Quenstedt.)

Fig. 16. *Mixosaurus* (?) *atavus* (Quenstedt). Two forms of teeth from the lower jaw, natural size. (After Fraas.)

The peculiar characters of the dentition of *Mixosaurus,* occurring as they have with other features which undoubtedly indicate a primitive stage of evolution, have suggested that possibly the dentition is essentially primitive, and that an original differentiated stage of a thecodont dentition which developed in the ancestors of the ichthyosaurs has been lost in the adaptation of the later forms, but is retained in the primitive *Mixosaurus.* If, as appears to be the case, the dentition of *Cymbospondylus* is not differentiated more than that of *Ichthyosaurus,* it may be that the differentiation of the mixosaur dentition was acquired in adaptation to a peculiar food habit; while the thecodont insertion, here as in most of the Triassic forms, may be a persistent or primitive character.

VERTEBRAE.

Vertebral Formula.—In the typical Ichthyosauria of the Jurassic the number of vertebrae in the spinal column shows considerable variation. In the genus *Ichthyosaurus* variation occurs principally in the posterior caudal region through the addition of small centra in the pinnigerous portion of the tail. The presacrals in *Ichthyosaurus* pretty constantly number between 40 and 46 with some slight variation from this number. An exception is found in the peculiarly specialized *I. platydactylus* Broili of the Cretaceous, in which the pelvis appears to have been near the 54th centrum. In *Baptanodon reedi* Gilmore the region of the pelvis is indicated at the 49th or 50th centrum, as the transverse processes reach their lowest position on the sides of the centra at this point. In *Opthalmosaurus* there are 40 presacrals, according to Andrews.[13]

Of the Triassic genera the complete presacral segment of the column is known only in *Mixosaurus* and *Cymbospondylus.* Judging from Repossi's figures there are between forty-five and fifty presacrals present in *Mixosaurus.* In a specimen of *Cymbospondylus* (pl. 7, fig. 1; no. 9950), including the complete presacral region, there are not less than 65 presacrals. In the type of *Delphinosaurus* (pl. 7, fig. 2) there are 40 presacrals present, and enough of the cervical region is absent to increase the number to between 45 and 50. In specimen 10998 (pl. 7, fig. 3) the vertebral column is complete to the posterior part of the skull, and there are about 40 presacrals present. As the region of the back of the skull is imperfectly preserved, there are probably several vertebrate not recognized, so that the total may be supposed to be the same as in the type specimen. In *Shastasaurus osmonti* (fig. 57) there are at least thirty-six vertebrae anterior to the region in which the rib articulation moves down from the upper portion of the lateral face of the centrum. As this downward movement occurs in all other ichthyosaurians near the middle of the dorsal region and generally fifteen or more vertebrae anterior to the pelvis (*Delphinosaurus* 15, *Cymbospondylus* 19 or more. *Ichthyosaurus* 15 or more) at least fifteen centra may be added to the thirty-six known in *Shastasaurus* making the number near 50. It appears then that in the known Triassic forms the number of presacrals is generally somewhat larger than in the typical *Ichthyosaurus.* That the number should be larger in these forms than in most of the later ichthyosaurs is rather remarkable, since the primitive reptilian types as the Diap-

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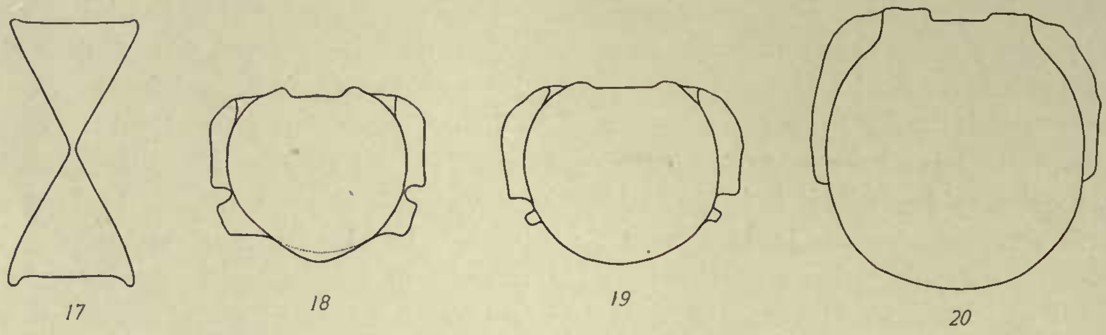
[13] Andrews, C. W., Geol. Mag., Dec. 5, vol. 4, p. 205.

tosauria and the Phytosauria, which have been suggested as ancestral to the Ichthyosauria, have in nearly all cases less than thirty presacrals.

The total number of vertebrae in the caudal region including the smaller centra at the end of the pinnigerous portion seems to be very closely represented in a *Delphinosaurus* specimen (no. 10998), and is approximately 75. In one of the Milan specimens of *Mixosaurus* the writer has counted about seventy-six vertebrae behind the posterior limb. In a large specimen of *Cymbospondylus* (fig. 132, no. 9947) a continuous series of 54 vertebrae is present behind the pelvis, and a part of the distal region of the tail is absent.



Figs. 17-20. *Shastasaurus osmonti* Merriam. Outlines of cervical and dorsal vertebrae, × ½. Fig. 17, anteroposterior section of 36th centrum; fig. 18, anteroposterior profile of 4th centrum; fig. 19, anteroposterior profile of 12th centrum; fig. 20, anteroposterior profile of 36th centrum.

In the caudal region the number of vertebrae anterior to the characteristic bend in the tail is, so far as known, nearly the same as in the later forms, or in some cases somewhat smaller. In the Milan *Mixosaurus* specimen possessing seventy-six caudals, the bend occurs near the twenty-fifth centrum behind the pelvis. On one specimen of *Delphinosaurus* (pl. 7, fig. 2) it is situated between the 25th and 30th vertebrae behind the pelvis, and in another (pl. 7, fig. 3) it appears to be between the 25th and 35th centra. In *Cymbospondylus* (fig. 132) the bend in the caudal region occurs at the 30th to 35th centrum behind the pelvis as it is situated here. This number is nearly the same as the number of centra that ordinarily intervenes between the pelvis and the downward bend of the tail in *Ichthyosaurus*.

Form of Centra.—The individual vertebral centra of all Triassic ichthyosaurians are biconcave as in later types. The biconcavity is so deep in some forms, as in the posterior dorsals of *Cymbospondylus* (fig. 24) or in the caudals of some of the small species from the Upper Triassic of Shasta County, that the middle portion of the centrum is perforated by a very small canal. The same character has been noted in the vertebrae of *Mixosaurus* (?) *atavus* by Fraas (1891, pp. 38 and 39) and was described by von Meyer[14] for

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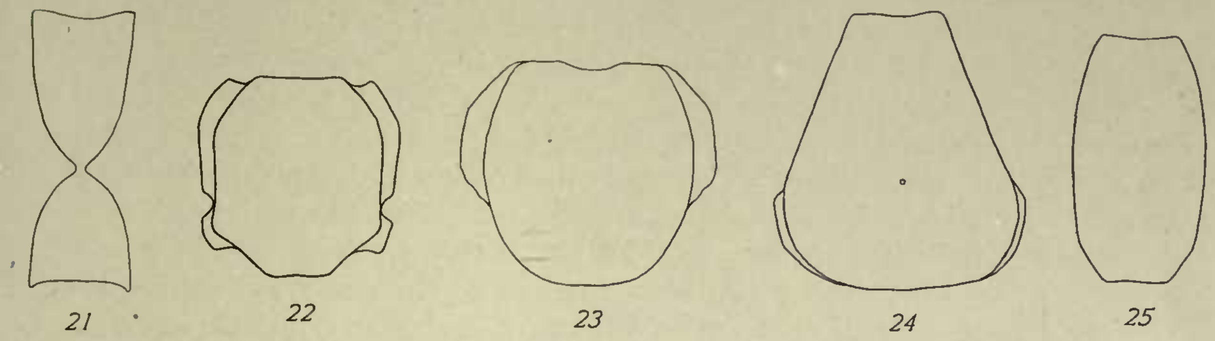
[14] von Meyer, H., Palaeontographica, Bd. 1, p. 253.

a Triassic vertebra probably belonging to an ichthyosaurian. Somewhat similar perforations appear occasionally in some of the later ichthyosaurs as in *Ichthyosaurus campylodon.*[15] In most forms the character of the excavation is similar to that in the typical species of *Ichthyosaurus* (fig. 17), the concavity beginning near the periphery of the centrum and sloping evenly toward the center. In *Cymbospondylus petrinus* (fig. 21), the best known Middle Triassic form, the outer portion of the articular face is nearly flat or only slightly hollowed, and the excavation cuts in sharply at about half of the distance to the middle. The flattening of the peripheral portion of the terminal faces is very pronounced in the posterior dorsal region.



Figs. 21-25. *Cymbospondylus petrinus* Leidy. Outlines of vertebrae, × ⅓. Fig. 21, anteroposterior cross-section of a dorsal centrum; fig. 22, anteroposterior profile of 3rd centrum; fig. 23, anteroposterior profile of anterior dorsal centrum; fig. 24, anteroposterior profile of posterior dorsal centrum; fig. 25, anteroposterior profile of posterior caudal centrum.

The occurrence of vertebrae in which the terminal faces are largely filled out in some of the earliest known ichthyosaurs naturally raises a question as to whether the deeply biconcave centra of the Upper Triassic and later genera are primitive, or whether they have been secondarily developed as a part of the adaptation to aquatic life. The more nearly solid centrum is evidently in general the type best fitted to meet the requirements in active land or shore forms. It has appeared in many of the reptilian groups, and even in certain of the more highly specialized Stegocephalia. Its development is possibly to some extent a function of size in the individual among land forms, as is indicated by its appearance in the large Stegocephalia and many reptiles; the deeply biconcave vertebrae persisting principally in the small land reptiles. In aquatic forms in which the vertebral column is relieved of a part of the strain of supporting the body the biconcave type of centrum may prove adequate. Of the specimens of the earliest European ichthyosaurs examined by the writer none have, however, been found to show such a degree of marginal flattening as is seen in

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[15] Kiprijanoff, W., Mem. L'Acad. Imp. des Sc., St. Petersb. 7 ser., t. 28, no. 8, p. 77. See also Dames, W., Zeit. d. deutsch. geol. Gesel. 1893 Bd. 45, p. 30.

Cymbospondylus, excepting the doubtful vertebrae described by von Meyer (Palaeontg. B. 1, p. 253). In the earliest forms from the Middle Triassic the centra are generally deeply biconcave, the concavity beginning at or close to the margin of the centrum. In *Mixosaurus* (fig. 121) a slight marginal flattening may be present, but it is not comparable to that of *Cymbospondylus.* As yet the extreme flattening in *Cymbospondylus* has been observed only on specimens of the large *C. petrinus.* In the type of *C. piscosus* (fig. 134) the concavity of the centra is like that commonly seen in *Ichthyosaurus,* so that large size may be an important factor in this case. On the other hand the enormous centra of *Shastasaurus careyi* from the Upper Trias exhibit no filling out of the intervertebral space. Among the more recent ichthyosaurians both perforation of the centrum and flattening of the peripheral portion of the terminal faces are occasionally seen, and appear together in *Ichthyosaurus campylodon.*

The proportions of the vertebral centra in the different regions of the column are in general much as in the ichthyosaurs of the Jurassic. The centra are generally broader than high in the cervical region, and gradually increase in height to the middle dorsal region, where the vertical and transverse diameters are nearly equal (figs. 18-20). Behind this point the transverse diameter becomes relatively small until in the posterior caudal region of some forms the height may equal three or four times the width.

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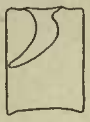
Fig. 26. *Delphinosaurus perrini* Merriam. Anteroposterior profile of anterior dorsal vertebra, × ½.

In the cervical and anterior dorsal regions the rib articulation extends upward over the superior margin of the centrum and covers a part of the base of the upper arch (fig. 26). In the posterior dorsal region it moves down to the lower margin, but rises again to about half the height of the side of the centrum near the middle caudal region. Particularly in *Cymbospondylus petrinus* (fig. 24) the posterior dorsal centra take on a sharply triangular form where the rib articulations reach the lower margin of the centrum.

The relative length of the anteroposterior diameter varies greatly among the Triassic genera. In some, particularly the latest, largest and most generally specialized forms the centra are relatively short and high, as is exemplified in *Shastasaurus careyi* (fig. 29), in which the length of a middle dorsal may equal less than 29 per cent. of the height. In all of the earlier forms the centra are relatively long. In *Delphinosaurus perrini* (fig. 27), found principally in a lower horizon than the forms with very short centra, the length of middle dorsal centra may equal 84 per cent of the height. The relatively great increase in height and width of the dorsal centra is paralleled to a considerable extent in the Cetacea. The extraordinary height of the centrum has been considered by

McGregor[16] as the probable reason why the ribs of ichthyosaurs do not articulate on the upper arches. It is true that in the small forms with relatively long and low centra, as in *Delphinosaurus,* the rib heads rest against the upper arches to a considerable extent. It is also true, that in several species of *Shastasaurus,* with vertebral centra as high and thin as in the typical *Ichthyosaurus,* the rib heads of the cervical and anterior dorsal region are in contact with the base of the neural arch.



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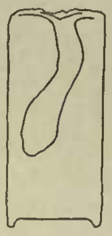

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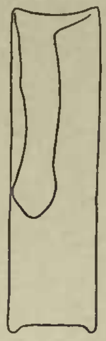

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Fig. 27. *Delphinosaurus perrini* Merriam. Lateral view of middle dorsal centrum, × ⅓.
Fig. 28. *Shastasaurus osmonti* Merriam. Lateral view of middle dorsal centrum, × ⅜.
Fig. 29. *Shastasaurus careyi* (?) Merriam. Lateral view of middle dorsal centrum, × ⅜.

Neural Arches.—The upper arches of the vertebrae in the Triassic genera seem in every case to be thicker transversely than in the typical *Ichthyosaurus.*

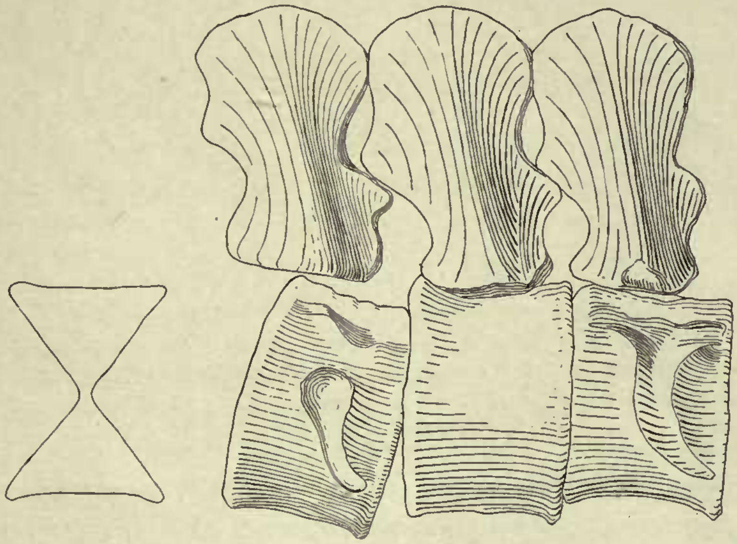

Fig. 30. *Delphinosaurus perrini* Merriam. Middle dorsal vertebrae situated at the point in the series where the diapophysial and neurapophysial surfaces of articulation are separated, × ¾.

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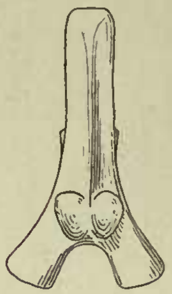
[16] McGregor, J. H., Mem. Am. Nat. Hist., vol. 9, pt. 2, p. 91.

The neural spines of the vertebrae of *Mixosaurus* (fig. 123) as figured by Repossi, appear to be thin and flattened distally, but a prominent rib is present along the lateral face of the arch, and extends for a considerable distance up on the side of the spine. In the cervical region of all the American Triassic forms the neural spines are so thick as to be nearly round in cross-section. In the dorsal region the spines may be greatly broadened anteroposteriorly and become quite thin distally (fig. 32*b*). This change from thick spines on the cervicals to broad, thin ones on the dorsals is well shown in *Delphinosaurus perrini* (pl. 7, fig. 2), but even in this form the lateral faces of the spines on the


31a


31b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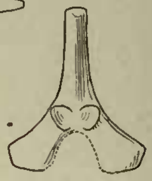
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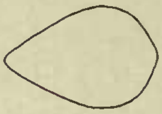
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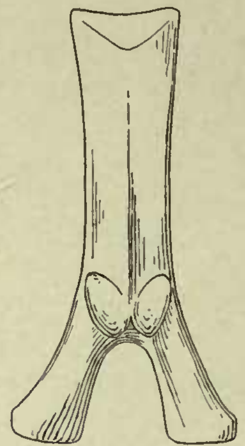
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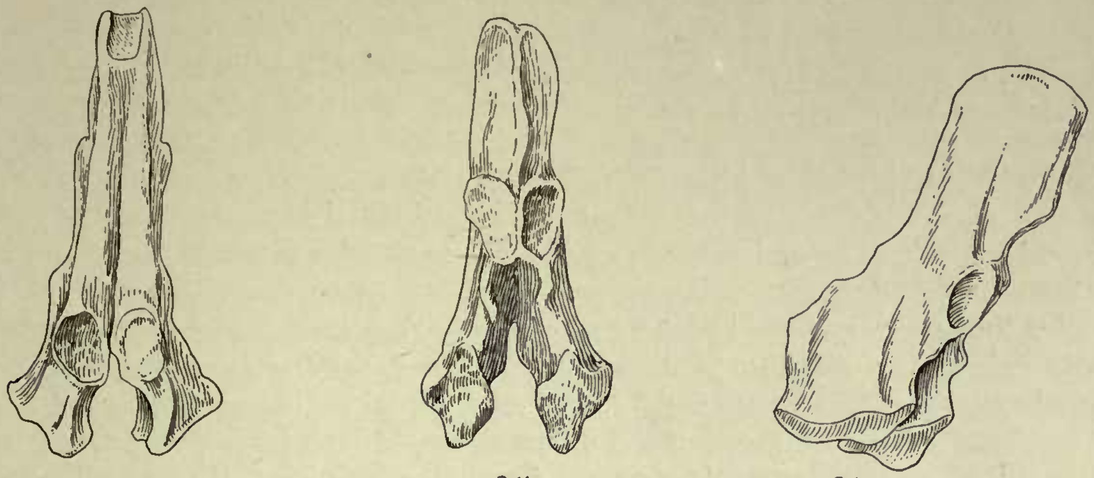
Figs. 31*a*-31*c*. *Shastasaurus osmonti* Merriam. Neural arch of a dorsal vertebra, × ½. Fig. 31*a*, lateral view; 31*b*, cross-section of summit of neural spine; 31*c*, anterior view.

Figs. 32*a*-32*c*. *Delphinosaurus perrini* Merriam. Neural arch of a dorsal vertebra, × ½. Fig. 32*a*, lateral view; 32*b*, cross-section of summit of neural spine; fig. 32*c*, anterior view.

Figs. 33*a*-33*c*. *Shastasaurus atispinus* Merriam. Neural arch of a dorsal vertebra, × ½. Fig. 33*a*, lateral view; 33*b*, cross-section of summit of neural spine; 33*c*, anterior view.

dorsals are each marked by a well-developed ridge (fig. 30). This lateral rib is situated in the middle of the lateral face of the spine, and possibly represents the original column of the spine from which the anteroposterior expansion has developed.

In *Shastasaurus altispinus* and *S. careyi* the spines show little transverse flattening in the dorsal region and sometimes none at all; but may be considerably thickened and perfectly circular in cross-section distally. In the type specimen of *S. altispinus* the middle dorsal spines seem to have thin, blade-like anterior and posterior expansions of no great width, for a short distance above the zygapophyses (pl. 18, figs. 2*a* and 2*b*). In a specimen of *S. careyi* (pl. 18, figs. 5*a* to 5*c*) the distal end of the spine is considerably thicker than the middle section, and shows no anterior or posterior blade-like expansions, but is circular in cross-section. In *S. altispinus* the terminal portion of the spine is hollowed out by an anteroposterior groove. In *S. careyi* it is evenly convex or domed.


34*a* 34*b* 34*c*

Figs. 34*a*-34*c*. *Mixosaurus* (?) *atavus* (Quenstedt). Neural arch of an anterior dorsal vertebra, natural size. (After Fraas.) Fig. 34*a*, anterior view; 34*b*, posterior view; 34*c*, lateral view.

In view of the fact that thickening of the neural spines is the rule among the Triassic Ichthyosauria, and is most persistent in the anterior portion of the vertebral column where the development of a sculling tail would have the least influence on the character of the neural spines, it is probable that the arches of the ancestral forms were of the round or thickened rather than of a laterally compressed type. The rounded type is occasionally found in aquatic forms, but is most common among running types.

In the cervical, dorsal, and anterior caudal regions zygapophysial facets are developed on the upper arches of all Triassic ichthyosaurs. As was first noted by Fraas (1891, p. 39), the facets of the zygapophyses in *Mixosaurus*(?) *atavus* differ from those of *Ichthyosaurus* in being distinctly separated and not situated in the same plane (figs. 34*a* to 34*c*). In the Jurassic forms the two faces are brought together at the median line and unite to form a single face (fig. 35). In all of American Triassic forms (figs. 31-33 and 36) the zygapophysial facets are large, distinctly separated, and inclined away from each other in the cervical and anterior dorsal region. In the posterior dorsal and caudal regions the facets may be considerably reduced and fall into nearly the same plane. This difference is evidently due to the fact that in the development of a broad, vertical sculling organ, the principal movements of the body have been sideways, and a union of the zygapophysial facets in one plane facilitated this movement. The normal form of zygapophysial articulation in which the anterior facets look toward each other would interfere to some extent with this motion. In the evolution of the group the tendency to change the zygapophyses naturally appeared first in the caudal region and was gradually carried forward toward the neck region. In the Middle Triassic forms the sculling tail was well developed and the zygapophyses of the posterior region of the column had already been considerably modified. In the cervical, and to some extent in the anterior dorsal region, the modification had not been very strongly expressed. The evidence of the zygapophyses can scarcely be interpreted as pointing toward any other than a land or shore type as the ancestral form of the group.

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Fig. 35. *Ichthyosaurus quadriscissus* Quenstedt. Neural arch with united zygapophyses, × ½. (After Fraas.)

Fig. 36. *Cymbospondylus petrinus* Leidy. Neural arch of 5th cervical vertebra, anterior view, × ½.

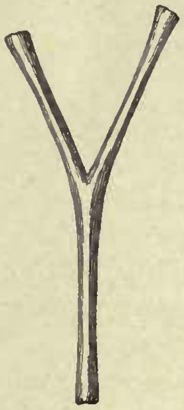

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Fig. 37. *Delphinosaurus perrini* Merriam. Inferior arch of anterior caudal vertebra, × ¾.

Hypocentral Elements.—The inferior or hypocentral elements of the caudal region furnish a most characteristic feature of all Triassic genera, and represent a less advanced stage in the development of the ichthyosaurian tail fin than in the post-Triassic forms. In every case where they have been observed the caudal hypocentra are united ventrally to form a long median stem (fig. 37), giving the inferior arches the Y-shaped form seen in the lower arches of the caudal series in most reptiles. In the type specimen of *Delphinosaurus perrini* (pl. 7, fig. 2) the chevrons are present from the anterior caudal region at least as far back as the bend in the tail.

In the ichthyosaurs of the Lower Lias of Europe (fig. 48, p. 43) the hypocentral elements are present, in many cases at least, considerably beyond the bend in the tail. According to Owen[17] they are not present on the terminal twenty or more vertebrae in *Ichthyosaurus.* In some of the Upper Liassic ichthyosaurs of South Germany, particularly in *I. quadriscissus* (fig. 49, p. 43), lower arches are not present in the region of the tail immediately in front of the bend, and have evidently in some cases disappeared entirely. In *Opthalmosaurus,* according to Andrews,[18] caudal intercentra appear to be present. In *Baptanodon,* according to Knight,[19] the lower arches are absent.

The history of the Ichthyosauria seems to give us a pretty definite trend of evolution of the hypocentral elements of the caudal region (figs. 43 to 49). It begins in the Triassic with forms in which the lower arches are of the normal chevron type. In the Lower Liassic ichthyosaurs the inferior union of the short paired elements has ceased. In the Upper Lias the hypocentra may disappear largely or in part, and in *Baptanodon,* one of the most recent genera of the order, they seem to have disappeared entirely.

The gradual modification and final elimination of the caudal hypocentra is undoubtedly to be ascribed to the increased efficiency of the terminal caudal fin. In the earlier ichthyosaurs the whole tail served as a sculling oar, and the elongated inferior arches heightened or broadened the tail. In later forms the flexure of the terminal portion of the caudal series made possible the development of a broad sculling organ in the region where it was most effective, and the power came to be applied largely in that region.

In the cervical region of *Shastasaurus* (fig. 57, p. 48) there are facets for an intercentrum between the third and fourth centra, making a fourth intercentrum not present in *Ichthyosaurus.* In this respect *Shastasaurus* may be considered more primitive than later genera. In the older *Cymbospondylus* there is, however, no intercentrum between the third and fourth vertebrae (fig. 58). The hypocentral elements of the cervical region are not known to be materially different from those of the Jurassic forms.

Atlas and Axis.—The atlas and axis are distinctly separated in all Triassic ichthyosaurs as far as known. In *Cymbospondylus* and *Shastasaurus* the adjacent faces of the atlas and axis are both concave and there is no suggestion of fusion as in the later ichthyosaurs. The atlas of *Cymbospondylus petrinus* (pl. 8 and text fig. 38) has about the same width and height, and about three-fourths the anteroposterior diameter of the axis. The anterior face is

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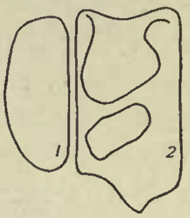
[17] Owen, R., Foss. Rept. Lias. Form., 1870, p. 92.

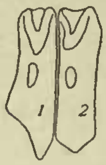
[18] Andrews, C. W., Geol. Mag., Dec. 5, vol. 5, p. 205.

[19] Knight, W. C., See Gilmore, Mem. Carnegie Mus., vol. 2, p. 107.

strongly convex, the inferior and lateral borders being much thinner than the superior side. The anterior face of the atlas shows no concave face into which the basioccipital might be received, but the posterior face of the basioccipital is deeply excavated for the reception of the atlas. The narrowed lateral borders have elevated anterior and posterior edges and show no indication of the presence of rib articulations. The upper arches of the atlas are formed much as in *Ichthyosaurus*.

In *Shastasaurus* (fig. 57) the form of the atlas is much as in *Cymbospondylus*, though the lateral borders are evidently not as sharply set off from the anterior face by an elevated anterior edge. A portion of an upper arch, apparently belonging to the atlas in the type specimen of *S. alexandrae*, resembles the neurocentral elements of *Ichthyosaurus*.





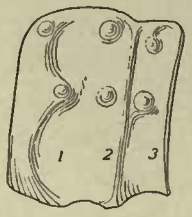


Fig. 38. *Cymbospondylus petrinus* Leidy. Atlas and axis, lateral view, × ⅓. 1, atlas; 2, axis.

Fig. 39. *Ichthyosaurus longifrons* Owen. Atlas and axis, lateral view, × ½. 1, atlas; 2, axis. (Adapted from Owen.)

Fg. 40. *Ichthyosaurus platydactylus* Broili. Atlas, axis, and 3rd cervical, lateral view, × ⅓. 1 and 2, fused atlas and axis; 3, 3rd cervical centrum. (After Broili.)

The axis of *Cymbospondylus* is in general like the succeeding cervicals, excepting in its marked inferior truncation for the hypocentral elements. It is characterized in some of the specimens examined (pl. 8, fig. 6) by the absence of parapophyses. The diapophyses of the axis are like those of the third centrum. The third vertebra shows large parapophyses. In *Shastasaurus* the rib articulation of the axis resembles that of the corresponding element in the later ichthyosaurs, and large parapophyses as well as diapophyses are present. Excepting in the two genera described above, the atlas and axis are not well known in the Triassic forms.

In the genus *Ichthyosaurus* the first two elements of the vertebral column are characterized generally by partial or complete fusion with each other and, so far as the information is available, there seems to be no indication of an intervertebral space remaining. The atlas and axis are also of nearly the same size (fig. 39).

In the latest members of the ichthyosaur group, as in *Baptanodon*, the fusion of the first two elements is complete, and the hypocentral element between them may disappear or lose its identity. In *Ichthyosaurus platydactylus* as recently described by Broili[20] (fig. 40), not only have the atlas and axis fused, but the third centrum is united with the second. In all of the Jurassic ichthyosaurs the centrum of the atlas is nearly or quite as large as the centrum of the axis (fig. 39), while the neurocentra rest upon it much as the elements of the upper arch of the axis. In this respect the atlas in these forms may be said to be more specialized than in most other reptiles. A possible explanation of the peculiar form and large size of the most anterior centrum here is that the anterior cervical centrum of the later ichthyosaurs may correspond to the axis of the earlier forms, the atlas having disappeared.

The known series of forms exhibiting the structure of the anterior portion of the vertebral column of the Ichthyosauria shows pretty clearly that progressive modification of the cervical region has taken place along somewhat the same lines that have been followed in the Cetacea. In the whales, fusion of the cervicals has reached an extreme stage, and the neck may be presumed to be much shortened. In view of the considerable difference between the Triassic and the Jurassic ichthyosaurs in the form and to some extent in the function of the most anterior centrum, it is possible that in a modification of the cervical region best adapting it to aquatic life, the neck has been shortened partly by elimination or by extreme reduction of the most anterior elements.

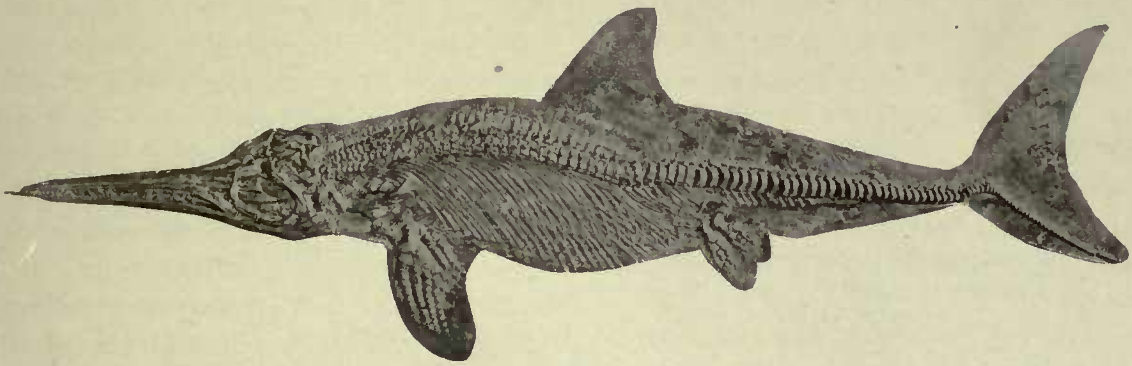


Fig. 41. *Ichthyosaurus acutirostris* Owen. Reversed photograph of a specimen in the Carnegie Museum. Reproduced by courtesy of Dr. W. J. Holland.

Caudal Fin.—In no other group of the reptilia have the functions of locomotion been so largely transferred from the limbs to the tail as we find them to be in the typical ichthyosaur. In consequence of this, the caudal fin of these forms has become the most specialized sculling tail known in the Reptilia. That it has reached the stage of evolution seen in the typical *Ichthyosaurus* (fig. 41) by passing through grades of development not unlike those of some

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[20] Broili, F., Palaeontog., Bd. 54, p. 143.

of the more generalized shore or fresh-water forms has been evident, but comparatively little information regarding the course of its evolution has been available.

In a specimen of *Ichthyosaurus trigonus posthumus* Wagner from the Upper Jurassic, one of the most recent of the well-preserved ichthyosaur specimens[21] exhibiting the impression of the epidermal investment of the caudal region, the caudal fin is seen to be broadly two-lobed with the distal end of the vertebral column turned sharply downward into the lower lobe (fig. 42). Traces of upper arches are seen on the vertebrae in the lower lobe of the fin, but lower arches seem to have been absent. The vertebral centra of the tail fin are very much smaller than those immediately in advance of the bend. They are also relatively very much longer anteroposteriorly, while the median portion is considerably constricted. The margins of the centra are thickened and rounded. Practically the same relations of the caudal vertebrae are seen in *I. platydactylus* Broili[22] of the Cretaceous. In some of the best specimens of *Ichthyosaurus* from the Upper Lias of South Germany (fig. 49), the downward bend is very pronounced, while the upper and lower vertebral arches are much reduced. The centra beyond the point of strongest curvature are not relatively much if any elongated. In these types the portion of the tail included in the terminal fin is large and the fin itself must have been capable of exerting considerable power. It was not supported to any extent by spinous projections of the upper or lower arches, but obtained its width largely through the bend in the caudal series. The paddles in these forms were too small to have furnished much power in swimming, and the hind paddles were so reduced as to be practically functionless.

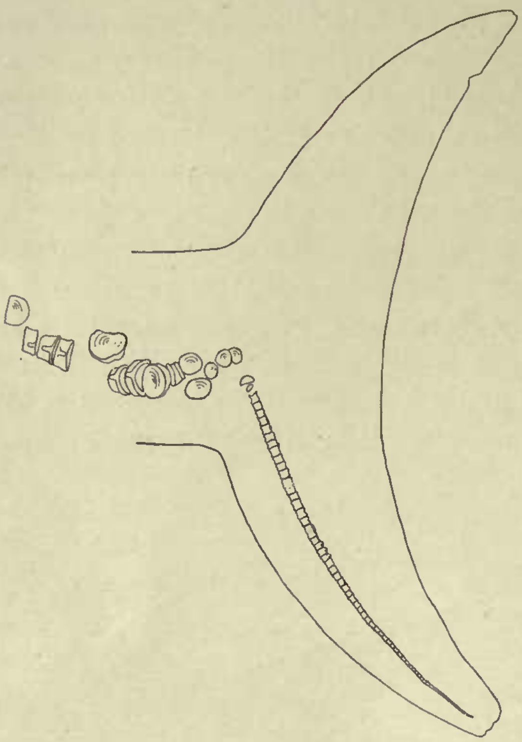

Fig. 42. *Ichthyosaurus trigonus posthumus* Wagner. Posterior caudal region with outline of the caudal fin, about 1/10 natural size. (After Bauer.)

In a number of the species of *Ichthyosaurus* from the Lower Lias of Eng-

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[21] Bauer, F., Palaeontog., Bd. 44, 1897-98, p. 309, and Taf. 27.

[22] Broili, F., Palaeontog., Bd. 54, p. 147.

land (fig. 48) the lower arches of the caudal series appear to be larger and extend out in the series to a point considerably beyond the bend in the tail. In these forms the area of the paddles is generally larger, and in many cases the posterior paddles are relatively large.

Among the Triassic ichthyosaurians the terminal portion of the caudal series is known in *Mixosaurus*, *Delphinosaurus*, and to a considerable extent in *Cymbospondylus*. Caudal vertebrae are also known from the other genera.

In *Mixosaurus* the well-preserved specimens at Milan show a structure which resembles that of *Ichthyosaurus* sufficiently to call to mind the type of tail fin present in the latter genus, but different enough to merit discussion as a distinct type (fig. 45). In this form the distal end of the caudal region was apparently not bent downward sharply as in the latest ichthyosaurs, but curved slightly upward near the middle of the caudal series and then down again some distance in front of the posterior end of the tail (fig. 50). This difference would not of itself attract attention so strongly were it not that the character of the vertebral arches in the flexed portion of the tail is very different from that in *Ichthyosaurus*. The neural arches instead of suffering gradual reduction as the point of curvature is approached, and disappearing very close behind it as in *Ichthyosaurus*, are considerably increased in length and stand erect in the curved region, and continue far back toward the terminal region of the series. In the Milan specimen best known to the writer the caudal region consists of about 76 vertebrae. The upper arches begin to turn forward at about the seventeenth centrum behind the posterior limb. The hypocentral elements are long, the inferior ends of the right and left pieces uniting to form Y-shaped arches. The writer has not seen lower arches immediately below the bend in the caudal series, but they are present and well developed behind the bend.

In a small specimen occurring in the same beds with *Cymbospondylus* in the Middle Trias of Nevada (no. 10624, fig. 44) practically the same relations of the elements of the caudal vertebrae appear as are found in *Mixosaurus*. The caudal centra are somewhat flattened laterally and bear apophyses, with which caudal ribs may have been in articulation. The neural arches are high and slender, their height equaling a little less than three times the height of the centra (× 2⅔). They show little if any anteroposterior curvature and stand nearly erect on the centra. The inferior arches are also long and slender, but are strongly recurved. Their length equals nearly two and one-half times the height of the centra. The articulation of each of the inferior arches seems to be mainly on a single centrum, instead of intervertebral. The union of the lower arches with the centra is so close that it may possibly amount to co-ossification in some cases.

In a large specimen of *Cymbospondylus petrinus* (no. 9947, fig. 46) there

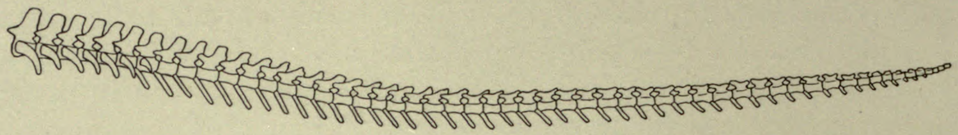


Fig. 43. *Palaeohatteria longicaudata* Credner. Caudal series, × ½. (Adapted from Osborn.)

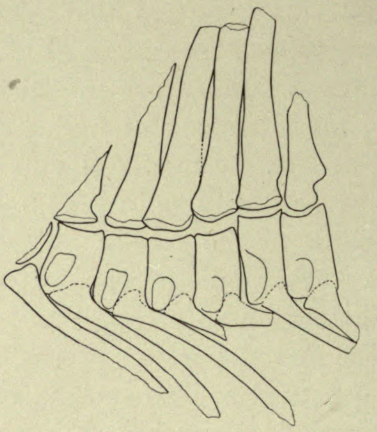


Fig. 44. *Cymbospondylus*(?) *natans* Merriam. Section of caudal fin, × ⅓.

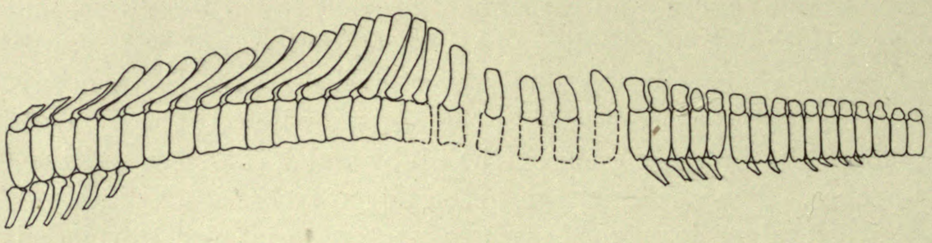


Fig. 45. *Mixosaurus cornalianus* (Bassani). Caudal series, × ½. (After Repossi.)

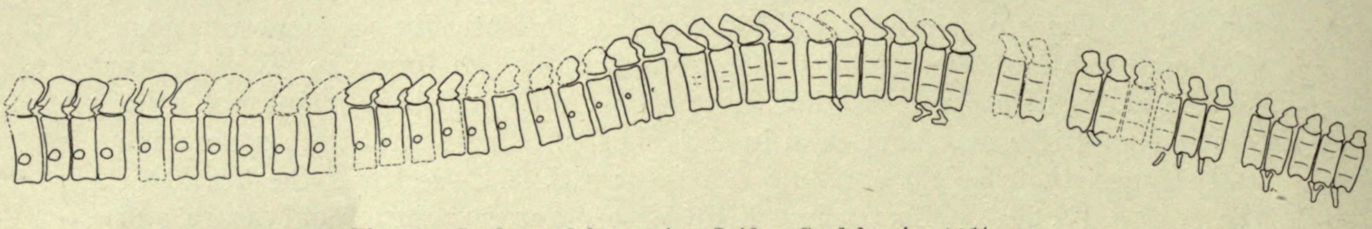


Fig. 46. *Cymbospondylus petrinus* Leidy. Caudal series, × $\frac{1}{15}$.

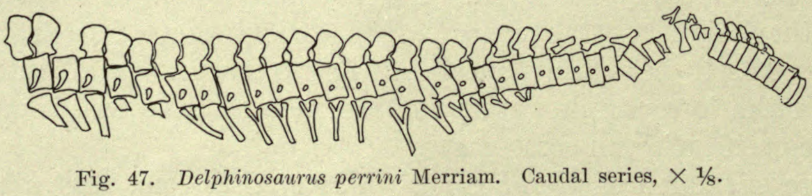


Fig. 47. *Delphinosaurus perrini* Merriam. Caudal series, × ⅛.

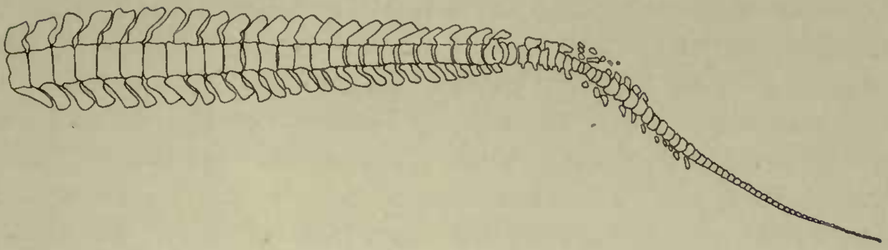


Fig. 48. *Ichthyosaurus intermedius* Conybeare. Caudal series, × $\frac{3}{16}$. (Adapted from Owen.)

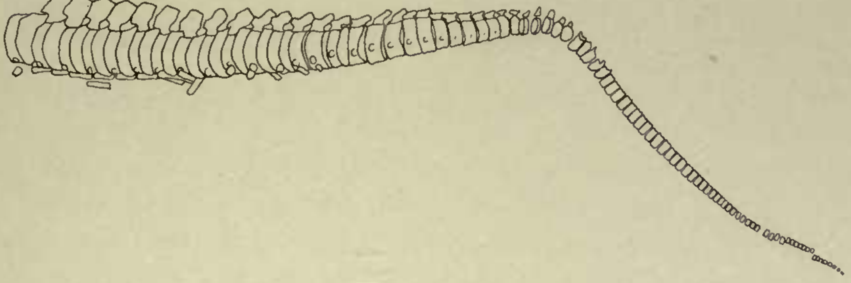


Fig. 49. *Ichthyosaurus quadriscissus* Quenstedt. Caudal series, about $\frac{1}{10}$ natural size. (After Fraas.)

is a continuous series of over fifty vertebrae showing the structure of the greater portion of the caudal region. At the thirty-fifth centrum in this series, which appears to represent a point normally thirty-five to forty centra behind the pelvis, a bend occurs in the tail. At this point the neural spines suddenly stand erect instead of inclining backward, and behind the thirty-fifth vertebra as far as the fifty-sixth they are inclined forward. The spines are not greatly elongated as in *Mixosaurus*, but keep a more nearly even height through the tail. At the thirty-fifth vertebra a change also occurs in the centra, which are considerably shortened inferiorly, indicating vertical curvature, and the diapophyses suddenly disappear. For some distance behind the thirty-fifth vertebra the centra increase somewhat in height and at the same time become absolutely narrower transversely. Small Y-shaped chevrons are present to the end of the series.

Fig. 50. Outline of the vertebral column of *Mixosaurus*. From rough sketch by the author.

In *Delphinosaurus* the caudal series shows a downward curve in the distal region not unlike that in *Ichthyosaurus,* though the bend is probably not so pronounced (fig. 47). The vertebral centra beyond the bend are small, but show some lateral compression, and are slightly higher than the centra immediately in front of the bend. Anterior to the bend in the tail the lower arches appear as long-spined chevrons. The chevrons are not certainly known behind the anterior region of the bend, but may have been present there. The upper arches of the centra in the anterior and middle region of the tail are of moderate height and are much flattened laterally. Immediately behind the bend the small upper arches turn sharply forward as in *Geosaurus* (fig. 52).

Fig. 51. *Clidastes velox* Marsh. Caudal series, × 1/12. (After Williston.)

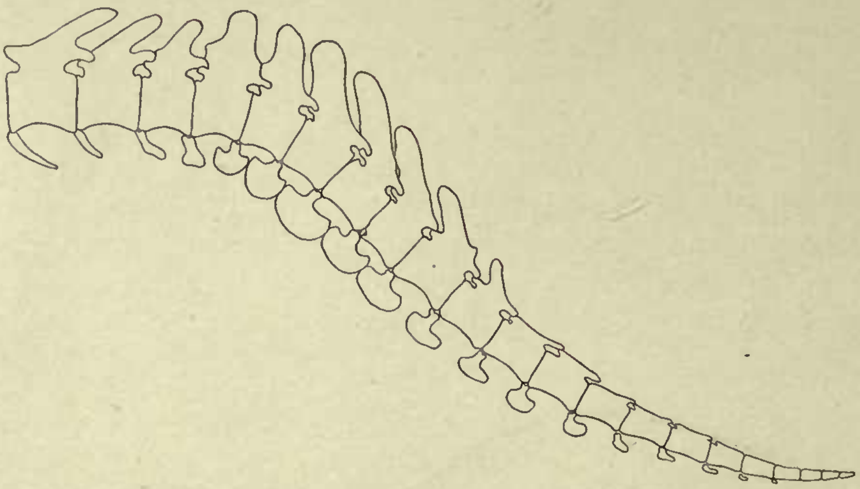


Fig. 52. *Geosaurus suevicus* E. Fraas. Caudal series, × ½. (After Fraas.)

The form of the caudal fin seen in *Mixosaurus* differs from that in *Ichthyosaurus* fundamentally in that the vertical expansion of the fin is produced in a large part by the elongation and erect position of the vertebral arches, whereas in *Ichthyosaurus* the arches have little or nothing to do with the widening of the fin. Sculling organs of a character somewhat similar to that of

Mixosaurus appear in other groups, particularly in the mosasaurian genus *Clidastes* (fig. 51), in which a portion of the caudal region somewhat in advance of the posterior end of the series is considerably broadened by the elongation and erection of the neural arches. The inferior spines are also somewhat elongated, and although fused to individual vertebral centra they are quite strongly recurved.

The modification of the caudal fin of *Clidastes* differs from that of *Mixosaurus* mainly in showing less evidence of vertical curvature of the distal portion of the vertebral column. If the tail fin of *Cymbospondylus*(?) *natans* were better known it would possibly be found to differ from *Clidastes* in general character less than does the corresponding region in the caudal series of *Mixosaurus.*

In the caudal fin of the typical *Cymbospondylus* the centra become higher and narrower beyond the bend, instead of smaller as in later forms, while the upper and lower arches are retained beyond the bend. The upper arches are inclined forward as in *Mixosaurus,* but are not extraordinarily elongated as in that genus and in *C.*(?) *natans.* Vertical expansion of the fin is produced in this instance partly by retention of the upper and lower arches, partly by increased height of the vertebral centra, and partly by vertical curvature of the column.

In the known history of the Ichthyosauria the caudal fin has passed through several fairly definite stages of evolution, and the trend of modification has always been in practically the same direction. The most primitive structure is probably that of *C.*(?) *natans* which leads to the type of *Mixosaurus.* In the large *Cymbospondylus* the structure is almost as primitive as in the other two Middle Triassic forms, the differences being possibly due in part to difference in size of the individuals compared.

Arranged in accordance with the hypothetical scheme of evolution of the ichthyosaurian caudal fin, the various known stages in the evolutionary series are, as shown on the following page, also arranged in the order of their appearance in time; excepting in the case of those Middle Triassic forms in which the factor of size is also to be considered. In the case of these Middle Triassic forms size has exerted the influence which could generally be predicted, the smaller forms showing the most primitive structure.

The fact that the known forms fall into a fairly definite series is not necessarily to be taken as indicating a single direct line of descent. They are widely scattered geographically, and differ sufficiently in minor details of structure to make difficult their arrangement in a single series. The fact that wherever the forms of a given period are found they seem to fall into this predicted position in the evolutionary scheme indicates all the more clearly the definite and long-continued tendency of evolution of the group in this particular.

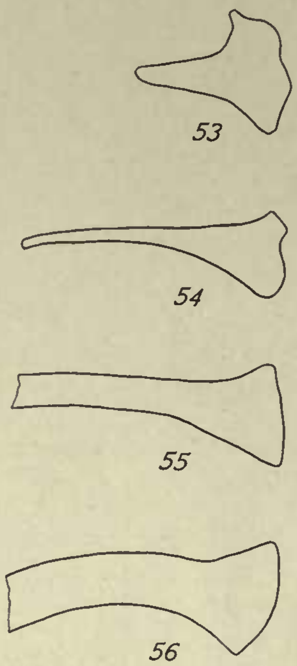
Including the hypothetical ancestors of the Ichthyosauria the following series of forms may be taken to represent stages in the evolution of the caudal fin:

1. Unknown littoral or terrestrial Permian ancestor with caudal series much as in *Palaeohatteria;* tail long, slender, not markedly expanded vertically, upper and lower arches imperfectly developed in posterior part of caudal series.
2. Unknown semiaquatic Permian or early Triassic ancestor. Caudal series long, tail considerably expanded vertically as in Crocodilia, upper and lower arches well developed excepting in terminal third or quarter of tail.
3. Early Triassic ancestor. Caudal series long, tail expanded vertically somewhat in advance of the posterior end by elongation or erection of the arches. Possibly represented by *Cymbospondylus*(?) *natans* or a closely allied form.
4. *Mixosaurus.* Middle or Upper Triassic form with distal expansion of caudal region caused in part by elevation of the vertebral arches, and in part by vertical curvature of the vertebral column.
5. *Cymbospondylus.* Large Middle Triassic forms possibly represented by preceding stages in the young animal. Distal portion of caudal region retaining short Y-shaped chevrons, and short erected neural arches; vertebral centra increased in height and laterally compressed behind the bend.
6. *Delphinosaurus.* Upper Triassic. Expansion of the distal portion of the caudal fin due largely to curvature of the vertebral column. Upper and lower arches considerably reduced in the region of the caudal flexure. Anterior caudal region relatively broad owing to the presence of laterally compressed upper arches of moderate size, and of long-spined chevrons.
7. *Ichthyosaurus.* Lower Lias. Much as in *Delphinosaurus,* but lower arches shortened and no longer united ventrally.
8. *Ichthyosaurus.* Upper Lias. As in Lower Lias, but with occasional almost complete reduction of lower arches.
9. *Ichthyosaurus, Opthalmosaurus,* and *Baptanodon.* Upper Jurassic and Cretaceous. Lower arches much reduced or absent, anterior and posterior margins of vertebrae behind the bend swollen, and with articulation faces swinging outward and somewhat backward on the swollen tracts. Centra behind the bend in the tail suddenly reduced in size. (In *I. posthumus* they become relatively small and long.) Posterior portion of caudal series more strongly deflexed than generally in preceding forms.

As has perhaps been evident in the preceding statement of the evolution of the ichthyosaurian caudal fin, the historical series of forms which is now available suggests that the peculiar upper lobe of the ichthyosaur fin originated at that period in the history of the group when the height of the tail was increased by elongation of the neural arches, and that once having taken on an important function it has been retained and enlarged.

Ribs.

In the Triassic ichthyosaurians, as in the typical *Ichthyosaurus*, rib articulations are present from the anterior cervical region along the whole of the vertebral column well out toward the distal region of the caudal series. Excepting the character of the rib articulation in certain regions, the general form of the ribs in the Triassic ichthyosaurs is not materially different from that in the later genera. The shaft is generally considerably flattened, excepting at the distal end, where it may be nearly round in cross-section. In all excepting the most anterior and posterior ribs the anterior and posterior sides of the shaft are more or less deeply grooved. Compared with *Ichthyosaurus*, the shaft is possibly somewhat shorter in the middle dorsal region of *Cymbospondylus* (pl. 7, fig. 1) and somewhat heavier in the dorsal region of some species of *Shastasaurus*.



Figs. 53-56. *Cymbospondylus petrinus* Leidy. Rib series, × ⅓. Fig. 53, anterior cervical rib; fig. 54, posterior cervical rib; fig. 55, anterior dorsal rib; fig. 56, middle dorsal rib.

In all of the American Triassic ichthyosaurs, excepting *Toretocnemus*, the ribs articulate on the vertebral centra and arches, with a single head excepting in the most anterior portion of the column (figs. 53-56).

In the best known specimen of *Shastasaurus* showing the vertebral column (fig. 57) the centra of the anterior cervical vertebrae show both diapophyses and parapophyses. The parapophyses are situated low down on the centra and are somewhat less than half the size of the diapophyses. In passing back toward the anterior dorsal region the diapophyses are seen to grow longer, while the parapophyses become much reduced. The distance separating the two apophyses remains nearly the same, or is at least not decreased. On the twelfth centrum of the series the parapophysis is a mere tubercle without an articular face. The last trace is seen on the eighteenth centrum, on which a rudimentary tubercle is present on one side only. Beyond the point of disappearance of the parapophyses, the diapophyses continue to increase in length but no division of the rib articulation appears.

In the older genus *Cymbospondylus* much the same relations of the rib articulation are seen, and the parapophyses are gradually reduced in passing back through the cervical series until they disappear entirely in the posterior cervical or anterior dorsal region. In one specimen (fig. 58) the parapophyses

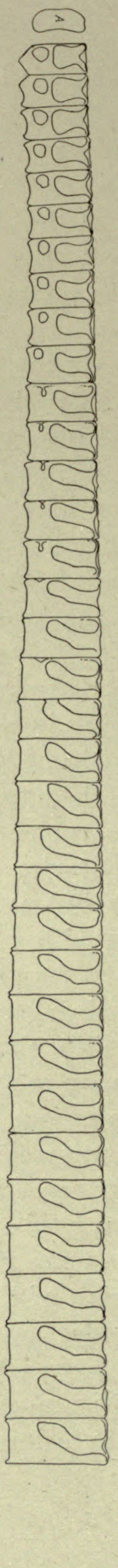


Fig. 57. *Shastasaurus osmonti* Merriam. Vertebral series of the type specimen, × ⅕. *A*, atlas restored from another specimen.

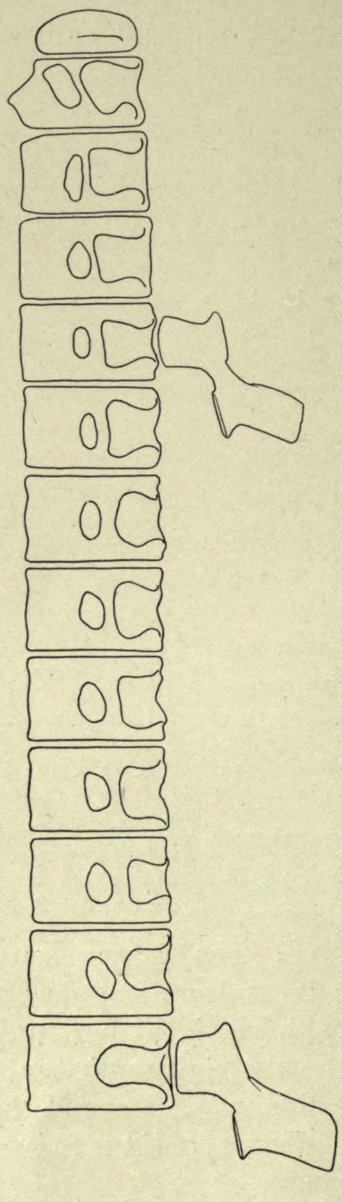


Fig. 58. *Cymbospondylus petrinus* Leidy. Vertebral series, × 2/9.

retain nearly the same size from the axis to the twelfth centrum. On the thirteenth the diapophyses are suddenly elongated, and there is no parapophysis on one side, though a rudiment is present on the other side. The diapophyses have a peculiar form on this centrum, the lower ends being turned backward instead of forward.

In *Delphinosaurus* the same relation obtains as in *Shastasaurus*, and in *Merriamia* we know only that the middle dorsal ribs are single-headed.

In *Toretocnemus* (fig. 59) the middle and posterior dorsal ribs have deeply notched or forked heads articulating on distinctly separated diapophyses and parapophyses. The vertebrae and ribs of the anterior region of the column are unknown.

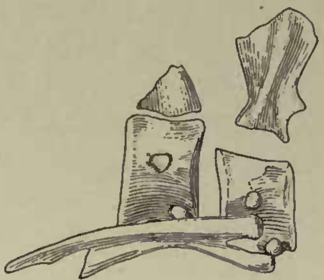
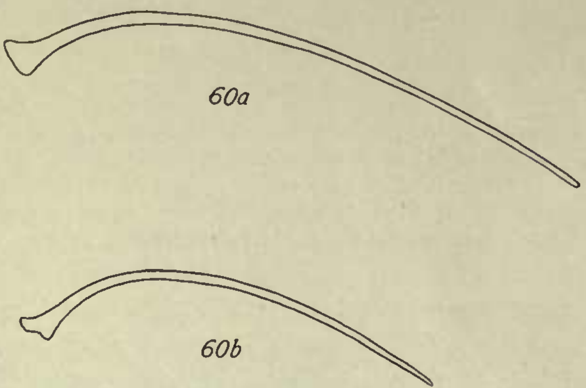


Fig. 59. *Toretocnemus californicus* Merriam. Vertebrae and rib from middle dorsal region, natural size.

In the European *Mixosaurus* the rib articulations are said to be unicipital excepting a possible faint division in the posterior dorsal and anterior caudal region (figs. 60*a* and 60*b*).

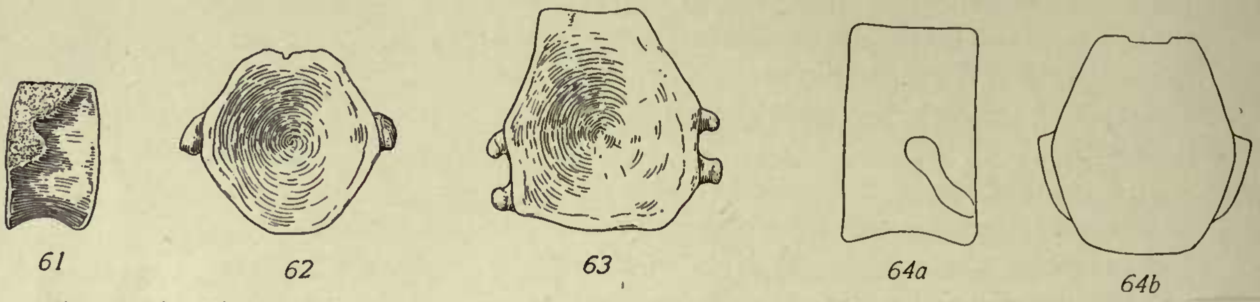
In *Mixosaurus*(?) *atavus* of the European Muschelkalk the only anterior dorsal vertebra known (fig. 61) seems to have a double-headed rib articulation. Several posterior dorsals from the collections at Stuttgart (fig. 63) and Zürich have distinctly separated diapophyses and parapophyses low down on the sides of the centra. Other centra (figs. 64*a* and 64*b*) not far from the region of the pelvis have a single, large, lateral apophysis in which there may be some indication of narrowing near the middle. These last centra show no traces of facets for intercentra, and if located behind the pelvis could not be situated very far from it.



Figs. 60*a* and 60*b*. *Mixosaurus cornalianus* (Bassani). Ribs natural size. (After Repossi.) Fig. 60*a*, dorsal rib; fig. 60*b*, posterior or anterior dorsal rib.

There are no vertebral centra available which certainly represent the middle dorsal region of *M.*(?) *atavus* unless some of those which have been referred to the anterior and posterior portions belong here. A peculiar centrum figured by Fraas (fig. 62) shows a cross-section similar to that of a middle dorsal, and possesses a small but prominent apophysis a little above the middle of each side. The writer has not seen so small an apophysis for unicipital articulation of middle dorsal ribs in any ichthyosaurs, but apophyses of this size, form, and situation occur in the middle caudal region. The centrum shows a central perforation. Such perforations appear to be more common in the caudal centra than in other regions of the column, but the nearly circular cross-section is not characteristic of the caudal region. If the centrum is an anterior dorsal the apophysis present is possibly the parapophysis, the tubercle having rested on the base of the upper arch.

That forms of rib articulation as different as those discussed above for *M.* (?) *atavus* occurred in the same region of the vertebral column in variations of the same species or even of the same genus seems improbable. It would therefore appear that we are dealing either with different parts of the vertebral column of similar individuals, or with quite different generic or specific types occurring together, as do *Toretocnemus* and *Merriamia* in the Upper Triassic of California. Apparently the only other possible situation in which either of the types of vertebrae referred to the posterior dorsal region could be placed would be the anterior caudal region; and that either form could be referred to this series is improbable as chevron facets are not present, and all other Triassic forms as well as most Jurassic ichthyosaurs possess well developed caudal hypocentra.



Figs. 61-64*b*. *Mixosaurus* (?) *atavus* (Quenstedt). Vertebrae natural size. Fig. 61, anterior dorsal or posterior cervical; fig. 62, middle caudal or middle dorsal; fig. 63, posterior dorsal; figs. 64*a* and 64*b*, from posterior dorsal or most anterior caudal region; figs. 61, 64*a*, and 64*b*, from rough sketches by the author; figs. 62 and 63, after Fraas; figs. 61-63, from specimens in the König. Naturalien-Cabinet, Stuttgart; figs. 64*a* and 64*b*, from a specimen in the Polytechnikum, Zürich.

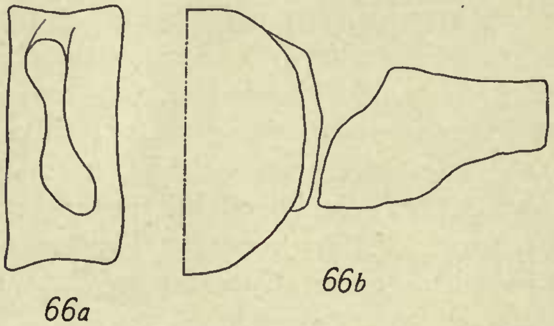
In the case of *Mixosaurus,* in which a division of the rib heads is supposed to occur in the caudal region, Yakowlew (1902, 2) has suggested that the rib articulations were originally single-headed, and that a division into two heads began in the caudal region owing to the influence of the peculiarly powerful lateral movements of the tail in swimming. Having in mind the desirability of determining the nature of the rib articulations in the pelvic region of *Mixosaurus,* the writer has examined a number of the excellent specimens at Milan. This examination shows that in some cases, at least, the short ribs near the pelvic region or the base of the tail have broad, undivided heads, as in the shastasaurian forms of the American Trias. In other instances ribs belonging to the anterior caudal region seemed actually to show a beginning division of the articular face. In one case, where the evidence seemed strongest, the apophysis on the vertebral centrum showed also some indication of division. It should, however, be noted that even in this instance the evidence hardly warrants a definite statement that double articulation occurs, as the side of the vertebral centrum is badly broken up, and does not present a satisfactory surface on which to make a thoroughly trustworthy observation. The heads of these ribs are moreover not fully exposed, and it is not impossible that further preparation with a needle will show that the apparent gap between the head and tubercle is filled by a bridge of bone covered by matrix lying in the extension of a lateral groove. It is also worth noting that ribs with heads formed as these appear to be as they are shown in the matrix, could not come into direct articulation with the diapophysis without elevating the shaft above the level of the other ribs.

In the case of the American Triassic genera, careful search has been made to determine whether any division of rib heads in the posterior dorsal or caudal region could be discovered in any type excepting *Toretocnemus.* In the posterior dorsal region the rib heads are found to be generally very broad, but show no indication of incipient division. In the caudal ribs no evidence of division of the head has been observed.

From the evidence available, some doubt must exist as to the true character of the rib articulation in the ancestral ichthyosaur. In all Triassic types excepting *Toretocnemus* and certain forms of the *M.*(?) *atavus* group the articulation is predominatingly unicipital. In all post-Triassic forms the articulation is mainly bicipital. If the double-headed articulation is primitive, such forms as *Cymbospondylus, Mixosaurus, Delphinosaurus,* and *Shastasaurus* are presumably not in the direct line of descent, and the later ichthyosaurs are probably to be derived from some such form as *M.*(?) *atavus* or *Toretocnemus.* If the unicipital articulation is primitive either *Cymbospondylus* or *Mixosaurus* might stand near the line of descent.

As far as the known relationships of the Ichthyosauria are concerned, there seem to be no particularly strong reasons for considering that either of the known types of articulation must be the primitive one. Single-headed ribs are perhaps the rule in the primitive Diaptosauria, but incipient bicipital articulation seems to be present in *Kadaliosaurus.* In the Phytosauria, which have been considered as probably very closely related to the Ichthyosauria, the rib articulation is markedly double-headed in the cervical and dorsal regions. If the ancestry of the ichthyosaurian group be pushed back far enough so that its origin may be considered to represent as early a date as that of the Diaptosauria, the ichthyosaurs must be supposed to have originated from some branch not far from the original cotylosaurian stem.

Excepting *Toretocnemus*, some of the *M.* (?) *atavus* specimens, and a doubtful division of the posterior dorsal and anterior caudal rib heads in *Mixosaurus*, double-headed articulation in the Triassic forms is limited to the most anterior region of the column, and in this region it becomes less pronounced in passing back from the most anterior cervicals. In the region of the thorax, where the ribs are long and are particularly influenced by the movements of the lungs, they have a single head. The Ichthyosauria being purely aquatic, high-sea animals may have remained under water for a considerable period at times, and have required a large intake of air before submergence, and full inspiration on returning to the surface. In the Cetacea, living under somewhat similar conditions, we find the most specialized forms showing a tendency to reduce the rib articulation of the dorsal region to a single head. This head is in the cetaceans, as in the shastasurian ichthyosaurs, the upper head or the one allowing the widest excursion of the ribs in inspiration. In the Cetacea it may be noticed also that the reduction of the lower rib heads takes place progressively forward, or occurs last in the most anterior ribs, as in *Shastasaurus*. In the shastasaurs a number of distinctly double-headed ribs have remained in the anterior region of the column. In the whales there being no cervical ribs the double articulation may show an apparently more extreme reduction.



Figs. 66*a* and 66*b*. *Shastasaurus altispinus* Merriam. Middle dorsal vertebra and rib, illustrating rib articulation, × ⅓. Fig. 66*a*, lateral view of centrum; fig. 66*b*, anteroposterior profile of centrum and rib.

In the Cetacea where the capitulum has become reduced, the tuberculum is usually only loosely attached, allowing the greatest possible movement. In *Shastasaurus* the single rib articulation of the dorsal region is marked by the development of an angle or prominence on the rib head and on the diapophysis. The articulations are so situated on both faces that the upper portion of the rib head and diapophysis turn away from each other, leaving a gap which was evidently partly filled in with cartilage or connective tissue (fig. 66). The cutting out of space between the upper portion of the rib and the diapophysis permitted a rocking movement of the rib head of such a nature as to allow extraordinary elevation of the distal end of the rib shaft, and without reducing the head to abnormally small dimensions.

A careful examination of the vertebral rib articulation in the cervical and anterior dorsal regions of *Shastasaurus* and of most specimens of *Cymbospondylus* suggests most strongly that in passing backward through the series the parapophysis is gradually disappearing, and the articulation is becoming solely tubercular or diapophysial. Yakowlew (1902, 1) has suggested that the bicipital articulation in Ichthyosauria has arisen through the splitting of single-headed ribs, or by atrophy of the median region of the head. If, however, the double-headed rib is derived from a single-headed form by reduction of the middle portion of the head, the reduction would probably not begin, as it does in the anterior dorsal region of *Shastasaurus,* by separation of a small and apparently functionless tubercle some distance away from the main rib head (fig. 57). The division would occur according to this method by gradual constriction of the rib head until a small space came to exist between two large and functional heads. Though such a condition occurs in other reptilian groups, it has not thus far been known to exist in the Triassic Ichthyosauria.

In *Shastasaurus* and *Cymbospondylus* the parapophyses generally remain about the same distance from the diapophysis no matter how large they are. Though the diapophysis gradually increases in height, the lower border never meets the parapophysis. In passing backward through the series the diapophyses gradually increase in size and the parapophyses decrease in size till the latter disappear, but at the point of disappearance the parapophyses are not absorbed into the diapophyses. The only case which might be considered as an exception to this rule is that of a specimen of *Cymbospondylus* (fig. 58) in which large parapophyses are present back to the twelfth centrum. On the thirteenth centrum the diapophyses are much increased in size, while the parapophysis has disappeared on one side and is represented only by a rudiment on the other side. The diapophyses on the thirteenth centrum are also of a peculiar form, being swung backward instead of forward. The parapophyses do not gradually approach the diapophyses on this specimen but are separated from them by a nearly uniform space.

If the double articulation has arisen from a single articulation in the forms described above it must have come in most cases through addition of an entirely independent rib head, and an inferior or parapophysial tubercle. This would mean that in the case of the rudimentary structures in the anterior dorsal region, both parapophysis and lower rib head appeared and developed to a considerable size before they could have any important function; and that the local conditions requiring a lower tubercle have progressed from the anterior cervical to the anterior dorsal region in *Shastasaurus,* or to the posterior dorsal region in *Ichthyosaurus* and *Baptanodon.*

In view of what has been said above, it seems less probable that the double articulation in the anterior dorsal region of the Shastasaurinae is incipient than that it is rudimentary; and it is possibly in order to consider the forms exhibiting this type of rib articulation as a side branch of the Ichthyosauria, which early developed a tendency to reduce the dorsal ribs to a single head.

Abdominal Rib Plastron.

Elements of the abdominal rib plastron are known with nearly all of the Triassic forms, but are in most cases scattered or disturbed to such an extent that their arrangement cannot be clearly determined. In one specimen of *Cymbospondylus petrinus* a portion of the rib plastron shown in fig. 65 was preserved without displacement of the elements. Each transverse series consists of a broadly V-shaped median piece and two lateral pieces. The median element is not divided into two parts as in some forms of *Ichthyosaurus*, but is produced forward as a prominent knob at the point of union of the lateral arms. All of the elements of the plastron seem to be heavier and more robust than in *Ichthyosaurus*. On this specimen there seem to be two transverse series of abdominal ribs for each pair of true ribs.

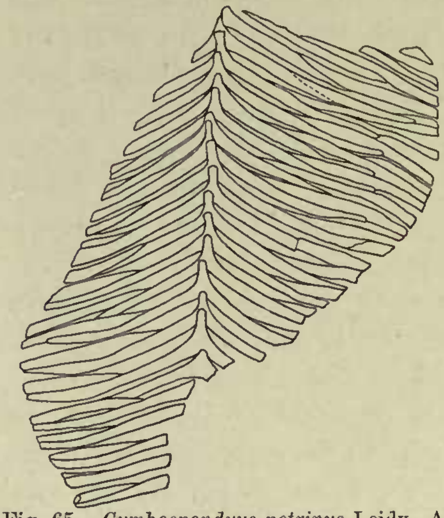


Fig. 65. *Cymbospondyus petrinus* Leidy. Abdominal rib plastron, × 3/20.

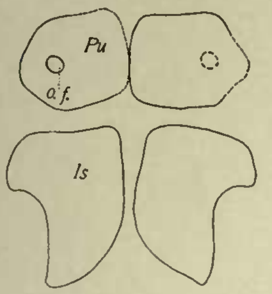
In *Mixosaurus* the nature of the abdominal ribs is, according to Repossi's figures (Repossi, 1902, tav. 8, fig. 1, and tav. 9, fig. 1), much as in *Cymbospondylus*, excepting that the elements are possibly less robust, and the anterior projection of the median pieces is acuminate, and is longer.

Limb Arches.

The Triassic Ichthyosauria differ generally from the later types in the closer agreement in size of the corresponding elements in the two limb arches. Though there are some notable exceptions, as in *Mixosaurus* and *Merriamia*, the anterior and posterior limbs, and consequently the pectoral and pelvic arches do not differ as widely in size as they are commonly seen to do in *Ichthyosaurus* and the later genera. A second difference generally distinguishing the arches of the earlier forms is found in the greater expansion of most of the elements, particularly of the pelvic arch. The large size and more robust character of the elements of the pelvic girdle are to be interpreted as directly indicating greater efficiency of the posterior limbs. The greater strength of the hind limbs probably indicates less effectiveness in the caudal fin. The anterior arch as a whole is heavy, but is not stronger than the arch of some forms of *Ichthyosaurus*.

Pelvic Arch.—In most cases the elements of the pelvis differ so far from the corresponding bones of post-Triassic forms that they might readily be considered as representing a quite different reptilian group. This is particularly true of the two inferior elements, which are much broadened, and show the expanded plate-like form seen in some of the most primitive reptilian types.

The ilium as known in *Toretocnemus* (fig. 69) appears to be considerably elongated and is relatively slender. In *Cymbospondylus* (fig. 70) the ilium is somewhat shorter and is considerably expanded distally. As seen in specimen 9950, in which the elements of the pelvic arch seem to have held together, the ilium is turned forward at the proximal end. Nearly the same form of ilium is present in *Delphinosaurus* (fig. 72) and *Shastasaurus* (fig. 73). In *Delphinosaurus* there is on the posterior side, near the proximal end, a small tubercle which does not appear in any of the other forms, and reminds one of the anterior extension of the upper portion of the ilium in land or shore forms with a strong sacral attachment.



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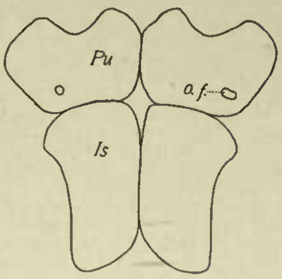

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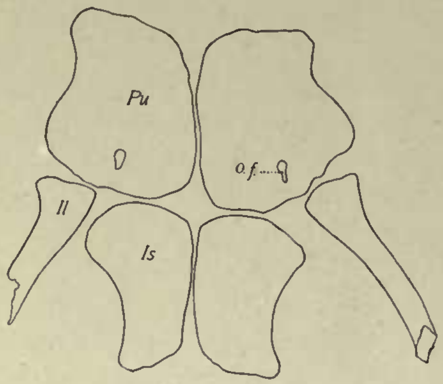

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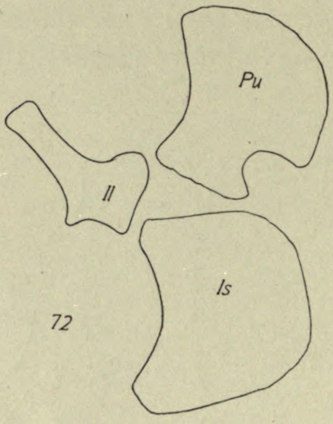
Fig. 67. *Procolophon trigoniceps* Owen. Pelvis, natural size. (After Broom.) *Pu*, pubis; *Is*, ischium; *O.f.*, obturator foramen.

Fig. 68. *Stereosternum tumidum* Cope. Pelvis, natural size. (After Osborn.) *Pu*, pubis; *Is*, ischium; *O.f.*, obturator foramen.

Fig. 69. *Toretocnemus californicus* Merriam. Pelvis, natural size. *Pu*, pubis; *Is*, ischium; *Il*, ilium; *O.f.*, obturator foramen.

All of the Triassic genera agree in the broad expansion of the distal portion of the pubis, but there is among them a considerable variation in the form of the proximal end of the bone. According to Repossi (1902, tav. 9, fig. 3), in *Mixosaurus* (fig. 71) the strongly curved median margin of the pubis bends into the proximal end of the bone without the formation of a hook, and there appears to be no opening corresponding to the obturator foramen. In *Toretocnemus* the pubis is very broad proximally as well as distally, and is perforated by an obturator foramen. In *Cymbospondylus* an obturator foramen may be present as in *Toretocnemus*. In some cases the opening may possibly



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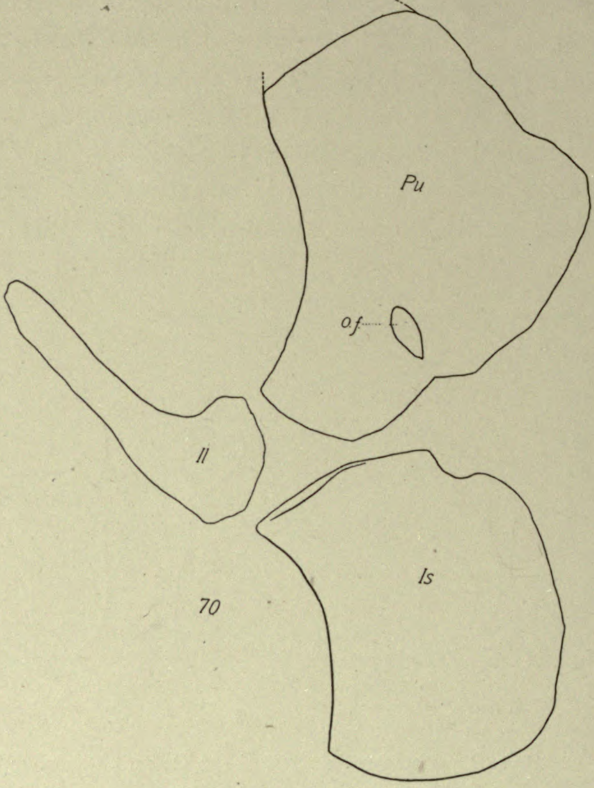

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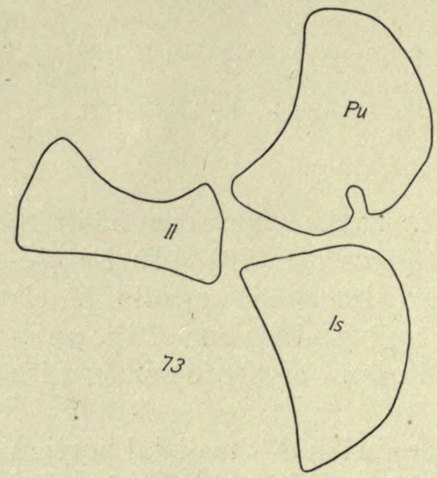

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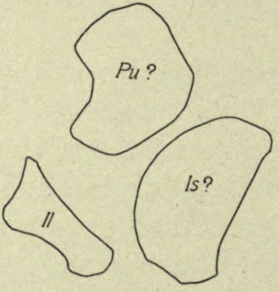

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Fig. 70. *Cymbospondylus petrinus* Leidy. Pelvis, × 2/9. *Pu,* pubis; *Is,* ischium; *Il,* ilium; *O.f.,* obturator foramen.

Fig. 71. *Mixosaurus cornalianus* (Bassani). Pelvis, natural size. (After Repossi.) *Il,* ilium; *Pu?,* pubis?; *Is?,* ischium?.

Fig. 72. *Delphinosaurus perrini* Merriam. Pelvis, × 1/2. *Pu,* pubis; *Is,* ischium; *Il,* ilium.

Fig. 73. *Shastasaurus osmonti* Merriam. Pelvis, × 1/4. *Pu,* pubis; *Is,* ischium; *Il,* ilium.

be incompletely surrounded by a broad, recurved hook formed by the much expanded median side of the blade as in *Shastasaurus*. In *Delphinosaurus* and *Shastasaurus* the pubis is much expanded distally, and the expanded middle portion curves backward so as to form a very prominent hook.

The form of the ischium is less variable than that of the other elements. In all cases it is an expanded plate-like element without distinctly marked tuberosities or constrictions. It shows the greatest transverse expansion in *Cymbospondylus,* in which in some instances the width almost equals the length (see fig. 134, p. 120). The narrowest form is seen in *Toretocnemus,* though the expansion is considerable even in that genus.

The character of the pelvis in the Triassic Ichthyosauria much resembles that of the early diaptosaurian reptiles, particularly in the nature of the inferior or ischio-pubic portion. The upper portion of the ilium is less robust than in the Protorosauria and Pelycosauria, but not less so than in the Proganosauria, Choristodera, and Rhynchocephalia. The pubis and ischium of *Toretocnemus* resemble the corresponding bones of *Stereosternum* (fig. 68) in all but minor details of outline, and so far as can be determined the ilium is also similar. In *Procolophon* (fig. 67) the inferior elements are like those of *Toretocnemus,* though the form of the pubis is more nearly circular. In *Champsosaurus* the ischium is similar and the pubis is perforated by an obturator foramen. From the inferior elements of the arch in *Palaeohatteria, Toretocnemus,* and *Cymbospondylus* differ mainly in the presence of a closed obturator foramen instead of an obturator notch. Excepting *Toretocnemus* and *Cymbospondylus* all of the American Triassic genera resemble *Palaeohatteria* in the general form of the ischium, and in the development on the pubis of a posterio-median hook bordering an obturator notch. Of the known forms, *Mixosaurus* is the only one in which neither foramen nor notch appears in the pubis, though otherwise the form of the element here differs but little from that in the other genera.

As has previously been suggested by the writer (1902, 2, p. 86), though the pelvis of the Triassic Ichthyosauria shows some resemblance to that of the Plesiosauria, the form shown here denotes mainly a less complete accommodation of the skeleton as a whole to aquatic conditions, than we find in the Jurassic ichthyosaurs. Koken[23] has seemed to imply that the plate-like pelvis of *Shastasaurus* is not primitive, but represents a peculiar accommodation.

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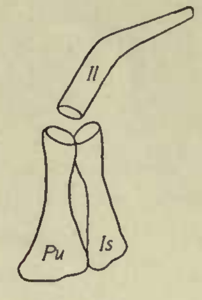
[23] Koken, E., N. Jahrb. f. Min. Geol. Palae. Bd. 1, p. 149, 1906.

''Das Becken von *Ichthyosaurus* ist nicht eigentlich angepasst; es durchläuft eine Reihe von Veränderungen, welche seinen Funktions-wert mehr und mehr herabsetzen; gerade bei *Shastasaurus* liegt Anpassung vor, wie bei Plesiosauriern, weil wahrscheinlich, das geht aus den Resten der kräftigen Hinterextremität hervor, diese ein wichtiges Lokomotionsorgan blieb.''

The view expressed by Koken is possibly not intended to be materially different from that of the writer as given above; though taken with the context it appears to be a criticism of the writer's suggestion that the form of the pelvis indicates ''less complete accommodation of the shastasaurian skeleton to purely aquatic conditions than we find in the Jurassic *Ichthyosaurus.*''

The question as to what constitutes a primitive character is not always readily determined, but it would seem that in this case there could be no misunderstanding. The course of evolution of the Ichthyosauria has led quite definitely up to a form in which the principal motive power came to be exerted through the caudal fin, and as the tail became more powerful the hind limbs were reduced in size and strength until their function amounted almost to nothing. In all of the recognized divisions of the Ichthyosauria, even in the specialized Shastasaurinae, the tendency to development of a powerful sculling tail seems to have been the same, and the ultimate result of evolution if continued long enough must have been the reduction of the hind limbs. In the course of this reduction of the limbs, the arches have been reduced, until in the latest type the rudimentary ischium and pubis are fused. Inasmuch as evolution of the particular kind seen in the ichthyosaurs leads to great reduction or loss of the pelvis, a posterior arch in which the elements have approximately the form and relative size seen in the primitive reptiles, and are associated with a large limb, may well be said to be more primitive than that of *Ichthyosaurus*.



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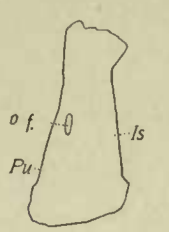

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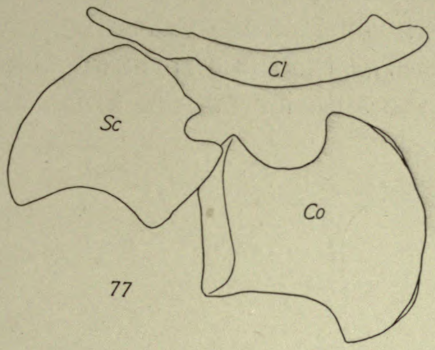
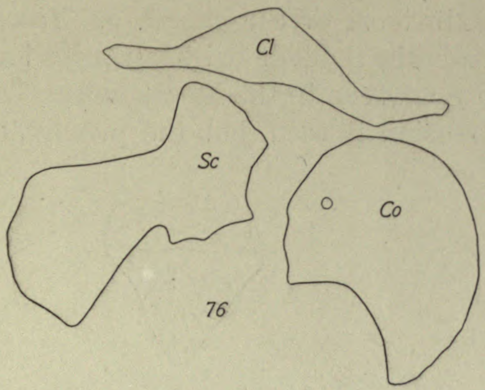
Fig. 74. *Ichthyosaurus communis* Conybeare. Pelvis, × ⅓. *Pu*, pubis; *Is*, ischium; *Il*, ilium. (After Woodward.)

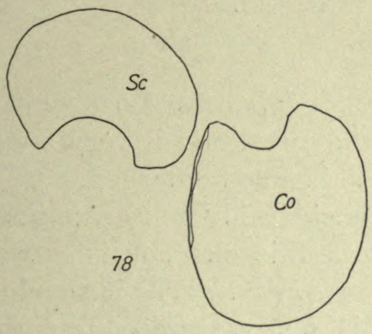
Fig. 75. *Opthalmosaurus icenicus* Seeley. Ischio-pubic bone, about ⅙ natural size. *Pu*, pubis; *Is*, ischium; *O.f.*, obturator foramen. (After Andrews.)

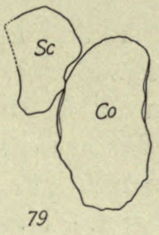
In the course of the reduction of the arch in the various divisions of the Ichthyosauria, it is to be expected that slightly varying forms would be assumed. That some of the variations which were in use while the posterior limb was large and functional might represent some slight phase of special adaptation is true, though the contention of the writer as previously expressed has not been that the pelvis itself was more primitive, but that it indicated less complete accommodation of the skeleton as a whole to purely aquatic conditions than we find in the Jurassic *Ichthyosaurus*. That the pelvis considered by itself might be assumed to be really more primitive than in the later Ichthyosauria appears also to be true, when we consider the extent to which the pelvic arches of all Triassic genera resemble the type of pelvis seen in most of the early Diaptosauria.

Pectoral Arch.—The shoulder girdles of the earlier ichthyosaurs resemble that of *Ichthyosaurus* in strength and compactness, but differ generally in the form of the individual elements. The only bone which is known to be constantly different is the scapula. This is always much expanded distally compared with the form in all post-Triassic species. The interclavicle, which is certainly known only from *Mixosaurus*, is nearly triangular, instead of T-shaped with a slender median stem as in the later genera. The coracoid and clavicle may resemble the corresponding bones in certain species of *Ichthyosaurus,* but are generally distinguished by features which are particularly characteristic of Triassic genera.









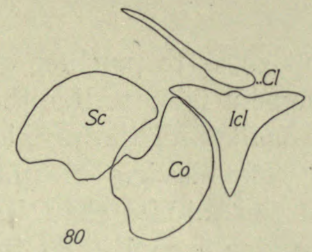


Fig. 76. *Cymbospondylus petrinus* Leidy. Pectoral arch, × 1/6. *Sc,* scapula; *Co,* coracoid; *Cl,* clavicle.

Fig. 77. *Shastasaurus osmonti* Merriam. Pectoral arch, × 2/9. *Sc,* scapula; *Co,* coracoid; *Cl,* clavicle.

Fig. 78. *Delphinosaurus perrini* Merriam. Pectoral arch, × 1/8. *Sc,* scapula; *Co,* coracoid.

Fig. 79. *Merriamia zitteli* (Merriam). Pectoral arch, × 1/3. *Sc,* scapula; *Co,* coracoid.

Fig. 80. *Mixosaurus cornalianus* (Bassani). Pectoral arch, × 1/3. *Sc,* scapula; *Co,* coracoid; *Cl,* clavicle; *Icl,* interclavicle. (After Repossi.)

In *Mixosaurus* and *Shastasaurus* the coracoid is narrowed or pedunculate proximally, as in *Ichthyosaurus communis* and in the early Liassic species generally. In *Cymbospondylus* and *Delphinosaurus* it is broadly sickle-shaped, the *Cymbospondylus* type being distinguished by an anterior perforation. In *Merriamia* the coracoid is nearly elliptical without constriction or emargination, somewhat as in *Ichthyosaurus integer.* As far as has been determined, the natural groups into which the Ichthyosauria of the Triassic seem to fall do not show more uniformity in the character of the coracoid than is seen in the ichthyosaurian groups represented in the Jurassic. There is, however, a general tendency toward narrowing of the proximal portion much as is common in the forms of the Lower Lias.

The scapula in all known Triassic ichthyosaurs is relatively broad distally, and in most of the genera as *Mixosaurus*, *Shastasaurus*, and *Merriamia* the broad distal blade with an anterior hook shows considerable resemblance to the form seen in the Mosasauria. In *Delphinosaurus* the same form of distal expansion is seen, but the proximal region of the anterior margin is not cut out so as to produce an anterior hook. In *Cymbospondylus* the form of the element is more like that in *Ichthyosaurus,* though the distal end is very much broader and the proximal region of the anterior side is much enlarged.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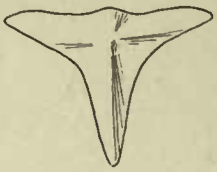
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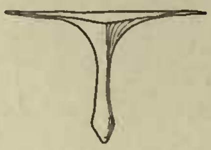
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Fig. 81. *Mixosaurus*(?) *atavus* (Quenstedt). Interclavicle, × ½. (After von Huene.)

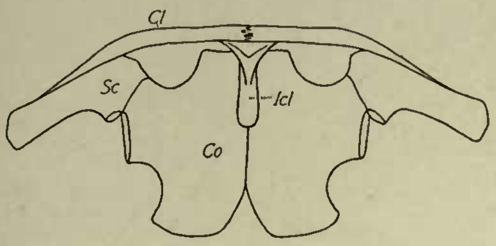
Fig. 82. *Mixosaurus cornalianus* (Bassani). Interclavicle, × ½. (After von Huene.)

Fig. 83. *Ichthyosaurus quadriscissus* Quenstedt. Interclavicle, × ½. (After von Huene.)

The clavicle of *Cymbospondylus* appears to be considerably more expanded in the middle than in other forms. In *Mixosaurus* this element is rather slender excepting at the median end. The clavicle of *Shastasaurus* is slender.

It is rather remarkable that the interclavicle is not recognized on any American specimen representing the Triassic Ichthyosauria; excepting possibly the type of *Merriamia,* in which its form is not clearly shown. In *Mixosaurus* it is markedly broader than in the later forms, and might better be denominated triangular than T-shaped as in *Ichthyosaurus.* Von Huene (1902, p. 11) has described from the Wellenkalk near Calev a thick triangular bone which he recognizes as an ichthyosaurian episternum. Placed in series with the interclavicles of *Mixosaurus* and *Ichthyosaurus quadriscissus,* as has been done by von Huene (figs. 81-83), there appears a very marked shrinking of the originally triangular element to the three radii of the triangle in *Ichthyosaurus.*

The shoulder girdle of the earliest known representatives in the Triassic was already considerably specialized in accommodation to the necessary functions of the fairly large paddles. The degree of specialization seen in this arch is probably greater than in the pelvis, inasmuch as the anterior limbs being farther away from the caudal fin, interfere to a less extent with the movement of the tail, and have a more definite and permanent value in the swimming mechanism of the animal. It might therefore be considered at the outset as a more difficult matter to determine affinities by the use of these elements than by comparison of the bones of the pelvis.



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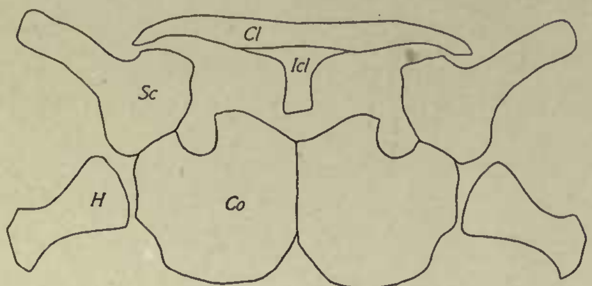

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Fig. 84. *Ichthyosaurus communis* Conybeare. Pectoral arch, much reduced. *Sc*, scapula; *Co*, coracoid; *Cl*, clavicle; *Icl*, interclavicle. (After Woodward.)

Fig. 85. *Baptanodon discus* Marsh. Pectoral arch, × 1/10. *Sc*, scapula; *Co*, coracoid; *Cl*, clavicle; *Icl.*, interclavicle; *H*, humerus. (After Gilmore.)

Probably, for the reasons given above, the anterior arch of the Triassic ichthyosaurs does not show the degree of correspondence with the pectoral girdle of early diaptosaurians that is generally evident in comparison of the posterior girdle with that of these forms. There is really no one of the diaptosaurian groups in which the correspondence is known to be as close in the anterior arch as it is in the posterior one. In *Stereosternum* (fig. 87) the anterior arch is not perfectly known, but the coracoid appears to be oval and imperforate in the young, and of somewhat similar form but perforate in the adult. The supposed scapulae of a young individual[24] are semi-lunar in form, and the interclavicle shows a diamond-shaped expansion at the anterior end of a long and slender shaft. In *Palaeohatteria* (fig. 86) the coracoids are small and discoidal, the interclavicle is closely similar to that of *Stereosternum,* and the scapula seems to differ mainly in the lack of excavation of the posterior border.

In comparison with the above forms the broadly triangular interclavicle of *Mixosaurus* suggests the expanded anterior end of this element in *Stereosternum* and *Palaeohatteria,* though the differences are considerable. The scapula of *Stereosternum* resembles that of *Delphinosaurus,* the broad perforated coracoid is a little like the perforated coracoid of *Cymbospondylus,* and the imperforate oval form corresponds to the type seen in *Merriamia.* There is no single ichthyosaurian form in which all of the characters of *Stereosternum* or

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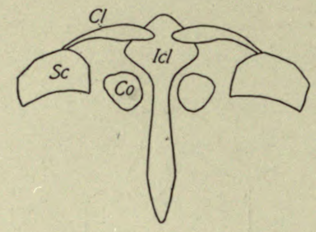
[24] Osborn, H.F., Mem. Am. Mus., vol. I, p. 487.

of *Palaeohatteria* are seen. As near an approach to the form of the pectoral girdle of a Triassic ichthyosaur as is known is found in the Proganosauria. In *Champsosaurus* (fig. 89) the girdle is not markedly different from the anterior arch of *Cymbospondylus* so far as known. The scapula has nearly the same form lacking only some of the distal expansion seen in *Cymbospondylus*. The coracoid of *Champsosaurus* is perforated as in *Cymbospondylus*, but is more nearly elliptical, instead of sharply excavated on the postero-lateral bor-



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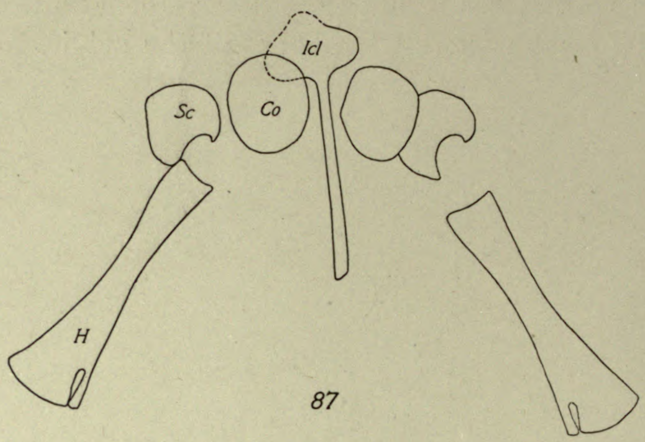

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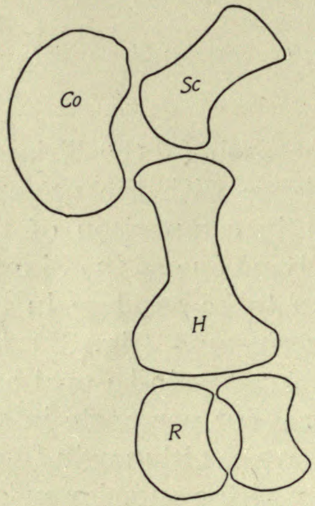

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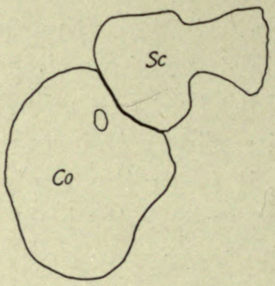

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Fig. 86. *Palaeohatteria.* Pectoral arch. *Sc,* scapula; *Co,* coracoid; *Cl,* clavicle; *Icl,* interclavicle. (After Credner.)

Fig. 87. *Stereosternum tumidum* Cope. Pectoral arch, × 2. *Sc,* scapula; *Co,* coracoid; *Icl,* interclavicle; *H,* humerus. (After Osborn.)

Fig. 88. *Thalattosaurus alexandrae* Merriam. Pectoral arch and limb, × ⅜. *Sc,* scapula; *Co,* coracoid; *H,* humerus; *R,* radius.

Fig. 89. *Champsosaurus laramiensis* Brown. Pectoral arch, × ½. *Sc,* scapula; *Co,* coracoid. (After Brown.)

der. The clavicles are large in both forms. The interclavicle of *Champsosaurus* is T-shaped as in *Ichthyosaurus,* but this element is unknown in *Cymbospondylus.*

The type of arch seen in the Triassic ichthyosaurs seems to approach most closely the form seen in the Diaptosauria, but owing to important changes in the functions of the anterior limb in adaptation to natation, it has come to vary considerably from that type in most cases.

LIMBS.

As early as the Triassic the amount of differentiation shown in the limb structure of the Ichthyosauria is surprisingly large, and apparently indicates that several fairly distinct lines of evolution or adaptation had been laid down. Excepting the greatly specialized shastasaurian species of the uppermost portion of the Upper Trias there is, however, in all of these varied forms an interesting group of characters which seem to interpret themselves only as persisting features of a primitive littoral ichthyosaurian with extremities having functions quite different from those of the true *Ichthyosaurus.*

In general the limbs of Triassic ichthyosaurians are distinguished by the following characters (see figs. 90-101): the epipodial elements are relatively long and are separated by a median space; in one or both of the epipodials there is a tendency to show a median constriction; the phalangeal region of the limb is relatively short; hyperdactyly never occurs; hyperphalangy is much less pronounced than in the later forms; the individual phalanges are relatively long, they are commonly notched on one or both borders even in the digits not situated on the borders of the limb, and may in many cases show a median constriction or shaft portion. Though it is not true of several of the genera, the hind limbs are generally relatively large. In *Toretocnemus* they appear to be fully as large as the anterior limbs. In *Cymbospondylus* and *Shastasaurus* they seem to have been almost as large.

While most of the above characters appear together in nearly all of the known Triassic forms, there have been developed in the Triassic some limb specializations which have eliminated certain of the primitive characters just mentioned. This is particularly true of *Shastasaurus,* which is, however, a very late Triassic form, and also represents a peculiar line of limb specialization apparently not present in the Jurassic genera.

As nearly as can be determined, at least two types of limb structure are represented in the Triassic genera. One form is seen in the broad paddle of *Mixosaurus* with a long podial[25] region, four proximal mesopodials, an alternating arrangement of the first and second rows of mesopodials, and five digits.

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[25] The word "podial" is here intended to represent the metapodial and phalangeal regions.

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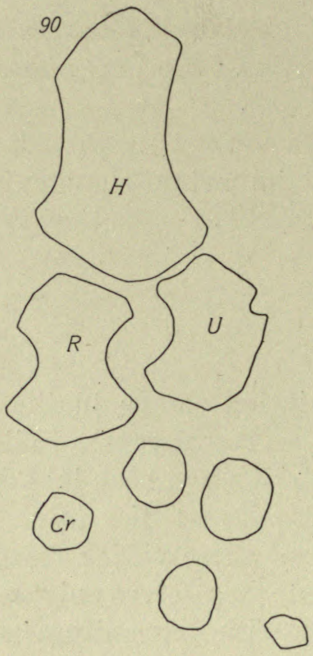

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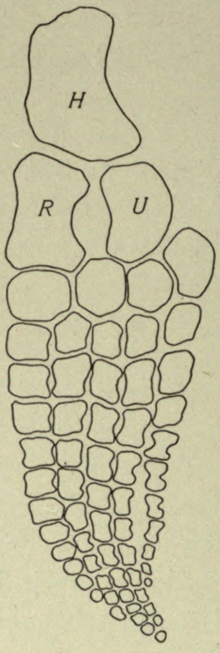

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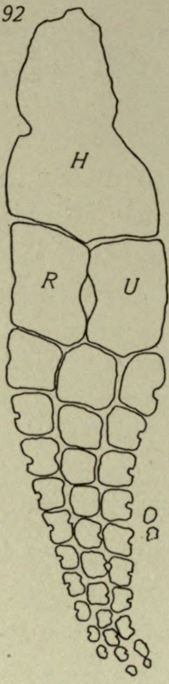

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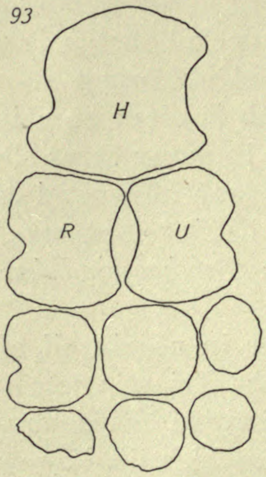

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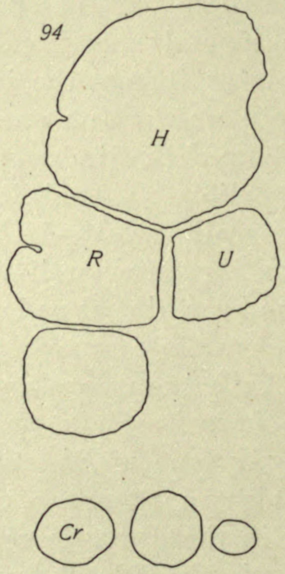

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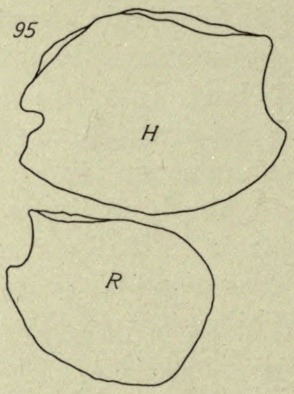

Figs. 90-95. Anterior limbs of Triassic ichthyosaurs. *H*, humerus; *R*, radius; *U*, ulna; *Cr*, carpal.
Fig. 90. *Cymbospondylus petrinus* Leidy, × 1/9.
Fig. 91. *Mixosaurus cornalianus* (Bassani), × 1/2. (After Repossi.)
Fig. 92. *Merriamia zitteli* (Merriam), × 1/2.
Fig. 93. *Delphinosaurus* perrini Merriam, × 1/3
Fig. 94. *Shastasaurus osmonti* Merriam, × 1/6.
Fig. 95. *Shastasaurus careyi* (?) Merriam, × 1/6

A second form is seen in the genus *Merriamia* with a narrow paddle, a relatively short podial region, three proximal mesopodials, a linear arrangement of the first and second rows of mesopodials, and but three functional digits. In both genera the characters mentioned appear in both anterior and posterior limbs. Of the four other genera recognized in the American Trias, *Delphinosaurus*, *Shastasaurus*, and *Toretocnemus* appear to have a type of limb-structure developed from some form like that seen in *Merriamia*. In *Toretocnemus*, in spite of the fact that the rib articulation is different from the other three genera, the limb structure is much like that of *Merriamia*. The American Middle Triassic *Cymbospondylus* may have a reduced phalangeal formula as in the Upper Triassic genera, and might be presumed to be related to these genera. It shows also a number of characters much like those of *Mixosaurus*, and may be nearer to that genus than are the American genera from the Upper Trias.

Mixosaurus and Cymbospondylus.—Probably the oldest limb elements known in the Trias, consist of some isolated mesopodial or podial elements and a humerus from the Muschelkalk of Germany. The humerus which was described by Fraas (1891, pl. 3, fig. 5) is not materially different from that of *Ichthyosaurus*. These specimens occur in the same beds with material referred to *M.* (?) *atavus* and probably belong in one of the forms included in that group.

Next to the lower Muschelkalk specimens of Europe, the earliest limb material is evidently that of *Cymbospondylus* (fig. 90) from the American Trias, closely followed in age by *Mixosaurus* (fig. 91) of the Italian Besano shales. The limb of *Mixosaurus* is fortunately preserved complete, showing all of the elements in position. In the known specimens of *Cymbospondylus* the podial region has not thus far been found undisturbed. These two forms represent the most primitive limb structure known in the Ichthyosauria. As the broad type of limb is possibly represented in one and the narrow type in the other, a comparison of the two is necessary in order to determine the common, or primitive characters.

The anterior and posterior limbs of *Cymbospondylus* were evidently not greatly different in size, the femur being apparently about one-sixth shorter than the humerus. In *Mixosaurus* the hind limb is relatively much smaller. The humerus and femur of *Cymbospondylus* are both relatively slender bones compared with the corresponding elements in other ichthyosaurians. In *Mixosaurus* the femur is slender, but the humerus may lack a median constriction, and have a transverse diameter almost equaling its length. In both genera the epipodial elements are relatively long compared with their own transverse diameter, or with the diameter of the proximal mesopodials. The radius is in both forms more slender than in other ichthyosaurian genera, and is much narrowed in the median or shaft region. In *Mixosaurus* the ulna is convex

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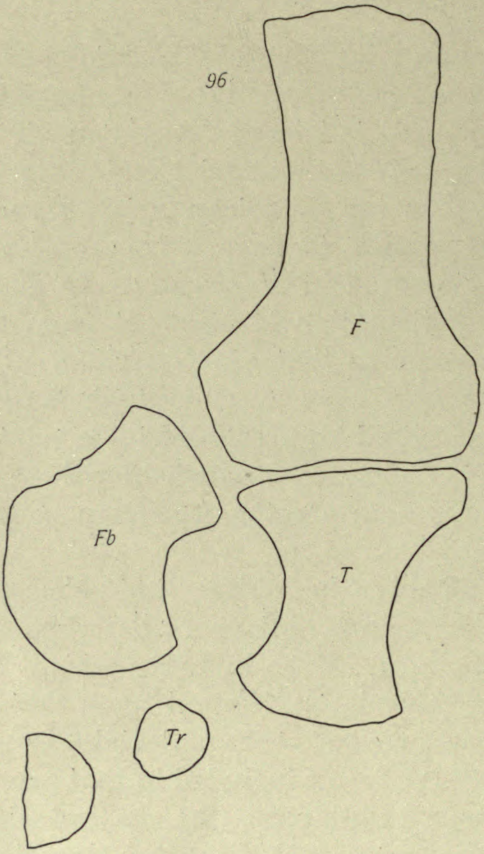

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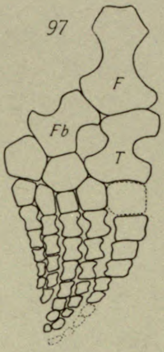

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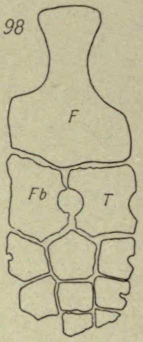

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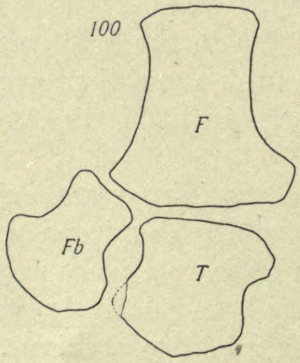

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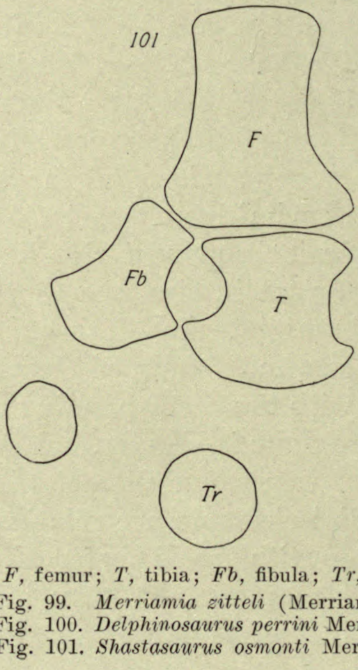

Figs. 96-101. Posterior limbs of Triassic ichthyosaurs. *F*, femur; *T*, tibia; *Fb*, fibula; *Tr*, tarsal.

Fig. 96. *Cymbospondylus petrinus* Leidy, × 2/9.
Fig. 97. *Mixosaurus cornalianus* (Bassani), × 2/3. (After Repossi.)
Fig. 98. *Toretocnemus californicus* Merriam, × 2/3.
Fig. 99. *Merriamia zitteli* (Merriam), × 1/2.
Fig. 100. *Delphinosaurus perrini* Merriam, × 1/2.
Fig. 101. *Shastasaurus osmonti* Merriam, × 1/4.

posteriorly, having expanded somewhat on this side, as in the limbs of most aquatic forms. In *Cymbospondylus* the posterior border is expanded, but still shows a portion of the median or shaft region that has not been filled out by lateral expansion.

In the posterior limb of *Mixosaurus* the propodial and epipodial bones are more slender, and more strongly constricted in the median region than are the corresponding elements of the anterior limb. In *Cymbospondylus* the femur is a little more slender than the humerus; the tibia is narrower distally than the radius, and the fibula has much the same form as the ulna.

In *Mixosaurus* the proximal row of the mesopodial region in the anterior limb consists of four elements of which the anterior three are the radiale, intermedium, and ulnare, in their normal positions. The fourth is a large pisiform set far up against the posterior margin of the ulna. In the typical *Cymbospondylus* three proximal elements are known but the form of the posterior side of the ulna suggests the presence of a pisiform as in *Mixosaurus*.

In *Mixosaurus* the podial region consists of five fingers, the number of phalanges in each of which is relatively small for an ichthyosaurian, not exceeding ten to eleven in the median digits. Many of the individual phalanges, particularly those in the proximal half of the phalangeal region and corresponding more nearly to the primitive phalangeal elements, are slightly elongated and show notches on one or both lateral margins, of such a form as to suggest an originally constricted shaft region.

In *Cymbospondylus* the podial elements have never been seen in complete series, but in several instances specimens representing parts of limbs show groups of three ossicles in rows, suggesting that possibly we are dealing here with transverse sections through mesopodial or podial regions with three digits. The borders of the rounded elements are not excavated or pitted as in *Shastasaurus*. (See figs. 112 and 113.) In one specimen an element similar to the doubly notched phalanges of *Mixosaurus* is associated with limb bones.

Considering the common characters of the limbs of these two genera, the oldest of the ichthyosaurian forms, both are seen to have more primitive epipodials than appear in any of the later genera. There is also some suggestion that in *Cymbospondylus*, as in *Mixosaurus*, a largely developed pisiform element was present and in articulation with the posterior margin of the ulna. In so far as they are known to differ, *Cymbospondylus*, apparently the older genus, is more primitive, the humerus being more slender and longer in comparison with the longitudinal diameter of the mesopodials; while the ulna remains narrower through failure to close the posterior notch by increase of the transverse diameter. Excepting those more primitive features of *Cymbospondylus* mentioned above, the limbs of *Mixosaurus* appear to be the most primitive ichthyosaurian extremities known, and may serve as representatives of the fundamental forms from which the modified structures seen in the later Ichthyosauria have been derived. Particularly is this true of the podial portion of the limb which is so well shown in the Italian mixosaur specimens.

Though the suggestion has been made that the most primitive form of limb in the Jurassic Ichthyosauria possesses less than five digits,[26] it is probable that the pentadactyl form seen in *Mixosaurus* is at least as near the primitive type as the limb of any known genus. The suggestion that the most primitive ichthyosaurian limbs have less than five digits is based on the supposition that the short first digit has disappeared. As the ichthyosaurian limb was already in *Mixosaurus* a highly specialized paddle it is to be presumed that if the first digit were to disappear at all, it would have been eliminated before the mixosaurian stage of evolution was reached. There are, therefore, the alternative hypotheses that the mixosaur paddle retains the primitive five digits and is the most primitive known, or that after having lost digit number one, it has brought the number of phalangeal rows up to five again by developing a digit not represented in the original five, and is therefore not a particularly primitive type.

In the development of the paddle in some aquatic animals there has been a tendency to eliminate the first digit, but this is by no means always the case. Judging from all the suspected relationships of the Ichthyosauria there is good reason to suppose that the ancestors of this group were forms possessing five digits. If such be the case, the general primitiveness of the mixosaurian limb, and the fact that this is the most ancient paddle of which the podial region is known, suggest that the digits seen here are the primitive five phalangeal series.

Another possibility, which should perhaps be borne in mind, is that the early ancestor possibly had only three or four digits. From what we know of the primitive reptilian groups this seems improbable, but the fact that all of the genera of the American Upper Triassic show a paddle structure of this nature, and that there is reason for suspecting the occurrence of a similar structure in the Middle Triassic *Cymbospondylus* lends some appearance of reasonableness to this hypothesis.

The form of the paddle and the arrangement of the mesopodial elements in *Mixosaurus* in some ways closely resemble the structure seen in the latipinnate forms of Ichthyosaurus (figs. 104 and 105). In both cases the paddle is relatively broad, and the third element of the second row of mesopodials articulates proximally upon the intermedium. In the longipinnate forms of *Ichthyosaurus* (fig. 102), as in the American Upper Triassic genera, the third element of the second row articulates with the posterior element of the first mesopodial row and not at all, or only incidentally, upon the intermedium.

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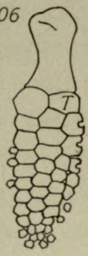
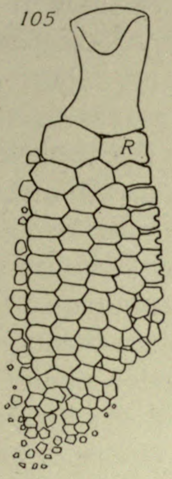
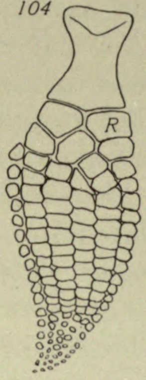
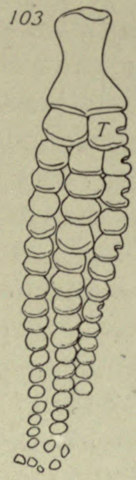
[26] Lydekker, R., Geol. Mag., 1888. Dec. 3, vol. 5, p. 310.









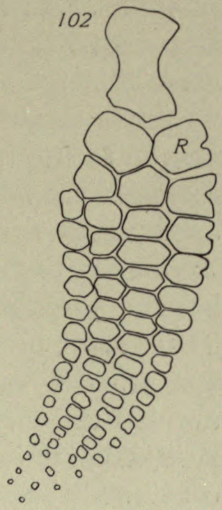


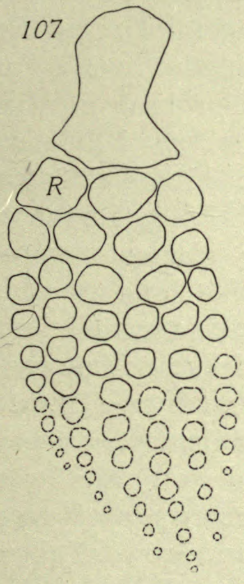
Fig. 102. *Ichthyosaurus quadriscissus* Quenstedt. Anterior limb, about ⅓ natural size. *R*, radius. (After Fraas.)

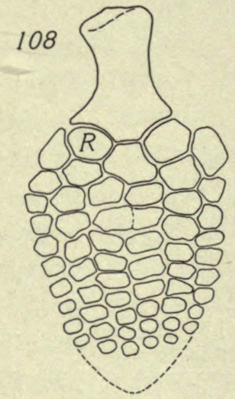
Fig. 103. *Ichthyosaurus acutirostris* Owen. Posterior limb, about ⅙ natural size. *T*, tibia. (After Fraas.)

Fig. 104. *Ichthyosaurus communis* Conybeare. Anterior limb, about ⅓ natural size. *R*, radius. (After Lydekker.)

Fig. 105. *Ichthyosaurus intermedius* Conybeare. Anterior limb, about ⅔ natural size. *R*, radius. (After Lydekker.)

Fig. 106. *Ichthyosaurus intermedius* Conybeare. Posterior limb, about ⅔ natural size. *T*, tibia. (After Lydekker.)





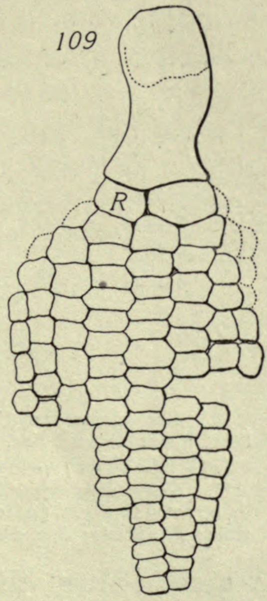


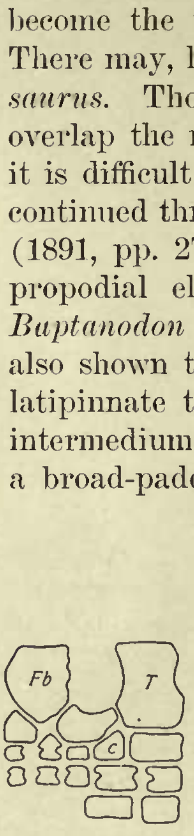
Fig. 107. *Baptanodon discus* Marsh. Anterior limb, about ⅛ natural size. *R*, radius. (After Marsh.)

Fig. 108. *Ichthyosaurus extremus* Boulenger. Anterior limb. *R*, radius. (After Boulenger.)

Fig. 109. *Ichthyosaurus platydactylus* Broili. Anterior limb, much reduced. *R*, radius. (After Broili.)

The structure seen in *Mixosaurus* appears more primitive than in the other forms, and seems also to show that no rearrangement of the digits has been made through addition to, or subtraction from the original number.

As to the definite relationship of the forms with the mixosaurian type of paddle to the typical Latipinnati of the Jurassic, and to the more specialized forms of the *Baptanodon* type, there may be some doubt, as the largely developed pisiform of *Mixosaurus* is not necessarily present in the Latipinnati. According to Baur's view (1887, 1) the pisiform of *Mixosaurus* has ultimately become the third or posterior epipodial element in *Baptanodon* (fig. 107). There may, however, be some question as to such a transition through *Ichthyosaurus.* Though a small proximal element of the posterior podial row may overlap the most posterior of the three elements of the first mesopodial row, it is difficult to demonstrate that the large pisiform of *Mixosaurus* has been continued through *Ichthyosaurus* to *Baptanodon.* As has been shown by Fraas (1891, pp. 27 and 30), the intermedium may come into articulation with the propodial element and thus furnish opportunity for development of the *Baptanodon* type of limb in any one of several groups. Boulenger (1904) has also shown that in *Ichthyosaurus extremus* (fig. 108) even though it be of the latipinnate type, the third element in articulation with the propodial is the intermedium. It is also interesting to note that Broili[27] has recently described a broad-paddled form (fig. 109) which he refers to the Longipinnati.



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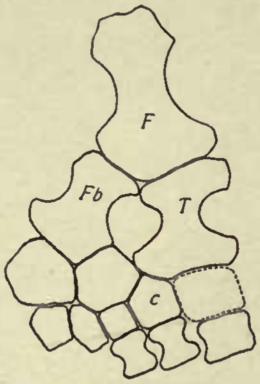

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Fig. 110. *Mixosaurus cornalianus* (Bassani). Posterior limb, about natural size, from rough sketch by the author. *T*, tibia; *Fb*, fibula; *C*, a distal carpal?

Fig. 111. *Mixosaurus cornalianus* (Bassani). Posterior limb, natural size. (After Repossi.) *F*, femur; *T*, tibia; *Fb*, fibula; *C*, a distal carpal?

Some suggestions as to the possibility of rearrangement of the elements of the mesopodial region are perhaps to be found also in the structure of the posterior limb of *Mixosaurus.* In the first row of the mesopodial section of the hind limb figured by Repossi (fig. 111), as in the anterior limb, four elements appear instead of three. The structure which appears in this case is unusual, but is probably explained by another specimen in the Milan museum (fig. 110) in which only three elements are present in the proximal row. The lunate intermediate element almost closes the gap between the tibiale and fibulare, but in a second row of bones three elements articulate with the distal border of the intermedium; of these the anterior one has crowded up between the tibiale and intermedium so as

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[27] Broili, F., Palaeontog., Bd. 54, p. 151.

almost to come in contact with the tibia. In the specimen figured by Repossi, this element of the second row seems to have reached the tibia. This explanation not only accounts for the fourth element of the proximal row, but may also explain the presence next the posterior border of tarsale one, and apparently functioning as tarsale two, of an element showing a strong median constriction. This bone has the appearance of a metapodial or phalange, and if the explanation given above is correct, is really a metapodial moved upward into the position of tarsale two.

Judging from the other relationships indicated in the characters of *Mixosaurus* there seems to be reason for considering that the genus is possibly not ancestral to any form of *Ichthyosaurus,* but is associated more closely with those forms in which the inferior rib head has been almost entirely lost. If such be the case, the broad type of paddle in *Mixosaurus* is evidently an independent expression of a tendency similar to that shown in the broad-paddled forms of *Ichthyosaurus.*

Merriamia.—The only Upper Triassic form in which the structure of the entire limb is known is the genus *Merriamia,* from the upper portion of the Upper Trias of California. In this type the manus (fig. 92) is relatively slender and includes only three functional digits with the faint rudiment of a fourth behind these. The humerus is relatively slender and shows a median constriction. The radius and ulna are one-half as long as the humerus and are separated by a large opening. Beyond the first row of the carpus, the limb elements are arranged in three well defined linear series, between which there is no interlocking. The metapodial and phalangeal elements are all more slender than in *Ichthyosaurus.* The elements of the two outer rows are all notched on the outer border, and in many instances a median constriction is developed. In the middle digit lateral notches are present only on the posterior border of the elements beyond the first phalange. Including the minute discoidal terminal elements, there are eight phalanges in the middle digit and seven in the first and third. In this genus the hind limb (fig. 99) is relatively small.

In contrast with the form of paddle seen in *Mixosaurus* that of *Merriamia* is exceedingly narrow, and the podial portion is also relatively short. The function of the paddle was evidently somewhat different from that in *Mixosaurus.* The relatively longer humerus and shorter podial region apparently gave the limb somewhat more freedom of movement than in the case of the limbs with shorter humerus and larger podial region as in *Mixosaurus* and other broad-paddled ichthyosaurians.

Toretocnemus.—The anterior limb of *Toretocnemus* is unfortunately known only in part (fig. 139), but in as much of it as is present the structure resembles that in *Merriamia.* Only digits one and two are preserved and in these the terminal phalanges may be missing, but the fourth element of digit one and the third of digit two are so small that the total number could hardly have been larger than in *Merriamia.* The posterior paddle in this genus (fig. 98) is also much like that in *Merriamia,* and the presence of a rudimentary fourth or posterior digit is indicated by small facets on the posterior margins of the elements of the third digit. In *Toretocnemus* the posterior limb is as large as the anterior one.

Delphinosaurus and Shastasaurus.—In both *Delphinosaurus* and *Shastasaurus* the propodial and epipodial limb elements are shortened as compared with the limb of *Merriamia.* In *Delphinosaurus* (fig. 93) the humerus is scarcely longer than broad, but retains a distinctly contracted shaft region. In *Shastasaurus* (figs. 94 and 95) the humerus may be so greatly abbreviated that its width considerably exceeds its length.

In *Delphinosaurus* the radius and ulna are of nearly equal size and the ulna differs from that of all other ichthyosaurs excepting *Cymbospondylus* in showing a posterior notch and a median constriction similar to that of the radius. In *Shastasaurus* the greatly shortened radius has a narrow notch on the anterior border while the posterior side is either only very slightly concave or is distinctly convex as in *S. careyi.* In that species is found the only exception to the rule that in the Triassic Ichthyosauria the radius and ulna are separated by a distinct cleft. In *Shastasaurus osmonti* the posterior border of the ulna is convex.

Although the phalangeal region of the limbs of *Delphinosaurus* and *Shastasaurus* has not been seen in its natural arrangement in connection with the remainder of the limb, there seems to be a strong reason for believing that it was of a reduced and presumably tridactyl type as in *Merriamia* and *Toretocnemus.* In *Delphinosaurus* where the radius and ulna are of nearly equal size, there are three elements each in the first and second rows of the mesopodial region as in *Merriamia,* but the posterior elements in both rows are much smaller than the others and much smaller than in *Merriamia,* suggesting that the posterior digit was relatively small. In *Shastasaurus* the radius is much larger than the ulna. The radiale, the only mesopodial which has been found in place, is considerably larger than in any of the other genera, and even exceeds the ulna in size. Evidently in this form the space for the posterior digits was considerably narrower than in *Delphinosaurus,* which suggests that *Shastasaurus* may have had only two well developed digits and a rudimentary third.

Though no series of paddle bones showing the form and arrangement of the elements in the podial region of *Shastasaurus* has as yet been discovered, in several cases a number of scattered bones representing mesopodials or phalanges have been found with other parts of the skeleton, but it has not been possible in any instance to make certain of their position in the paddle. With specimen 9081 a number of discoidal bones are associated with the elements of the shoulder girdle and the proximal portion of the limb. Three of these not far from the radius appear from their position to represent a transverse row from the proximal portion of the paddle (*Cr.* fig. 94). At one end of the row the ossicle is much smaller than either the median one or the one at the opposite end. While it is not possible to make sure whether the elements seen here belong in the podial or in the mesopodial region, the evident reduction of one of the terminal bones supports the evidence for reduction of the third or posterior digit as suggested above.

In several of the specimens of *Shastasaurus* discoidal ossicles present with the limb elements are deeply pitted or grooved around the margins (fig. 113; also pl. 15, figs. 3 and 4). This structure, with the circular outline developed, evidently indicates that they were embedded in heavy cartilage plates as in *Baptanodon* (fig. 114). The only instance in which other than discoidal elements have seemed to represent the distal portion of the paddle in *Shastasaurus* is in the type specimen of *S. altispinus* (pl. 18, fig. 4), in which there are two ellipsoidal bones sharply notched at one end, but with the margins grooved and pitted. The notches evidently indicate that the bones were on the margins of the paddle.


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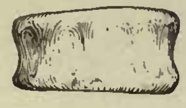
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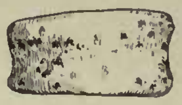
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Fig. 112. *Cymbospondylus petrinus* Leidy. Metapodials or phalanges, × ½.
Fig. 113. *Shastasaurus osmonti* Merriam. Metapodial or phalange, marginal view, × ¾.
Fig. 114. *Baptanodon* sp. Phalange, marginal view, × ¾.

In both *Delphinosaurus* and *Shastasaurus* the femur is more slender than the corresponding elements of the anterior limbs. (See figs. 100 and 101.) The tibia is relatively large compared with the small fibula. Both tibia and fibula show a median constriction. Of the elements beyond the epipodials only a few discoidal ossicles are known.

STAGE OF EVOLUTION OF TRIASSIC ICHTHYOSAURS.

In viewing the Ichthyosauria collectively there seems to be no reason for questioning the unity of the group. Throughout the entire series of forms in which the history of the order is represented there is no doubt as to relationship; the oldest and the youngest members showing so strong a resemblance to the typical genus that no question as to their common descent has arisen. In comparing the oldest forms with the latest there is, however, a strong contrast in the structure of many of the important parts of the skeleton, and the differences are of such a nature and so graded in time as to suggest progressive specialization of a very definite type.

A list of characteristics in which the Triassic and the later Jurassic ichthyosaurs are found to differ would include the following:

LATER JURASSIC FORMS.	TRIASSIC FORMS.
1. Locomotion almost solely by means of powerful vertical caudal fin.	1. Locomotion assisted to a greater extent by paddles than in the Jurassic forms.
2. Limbs much abbreviated, and functioning largely as fins rather than as paddles. Epipodials reduced to the form of mesopodials.	2. Limbs relatively large and with important function as paddles. First two segments relatively long.
3. Hind limbs relatively small.	3. Hind limbs relatively large.
4. Epipodial, metapodial, and phalangeal elements reduced to polygonal plates, or to approximately circular discs with concave margins.	4. Epipodial, metapodial, and phalangeal elements often elongated, and with shafted median region.
5. Number of phalanges in each digit greatly increased.	5. Number of phalanges in each digit relatively small.
6. Number of digits often greater than five.	6. Number of digits not increased beyond five.
7. Pelvis much reduced: in later forms with ischium and pubis fused.	7. Pelvic elements heavy: inferior elements much expanded. Ischium and pubis never fused.
8. Pelvis loosely connected with body.	8. Upper end of ilium broad, indicating somewhat firmer connection with vertebral column than in *Ichthyosaurus*.
9. Skull much elongated, and relatively large compared with the trunk.	9. Skull shorter compared with length of the trunk.
10. Jaws slender and much elongated.	10. Jaws generally relatively short.
11. Maxillaries relatively small; premaxillaries relatively large.	11. Maxillaries relatively long, and premaxillaries relatively short.
12. Orbits greatly enlarged. Superior temporal opening small, bar behind orbit very narrow.	12. Orbits relatively small, temporal bar behind orbit broad.
13. Auditory apparatus consisting of massive elements adapted to use in deep diving.	13. Element supposed to represent stapes relatively small.
14. Teeth numerous, simple-conical, loosely attached.	14. Teeth numerous in *Cymbospondylus*, relatively few in *Mixosaurus*. Teeth set in pits in older forms.
15. Vertebral centra high, relatively short anteroposteriorly.	15. Vertebral centra averaging relatively long and low.

16. Neck short, usually with two or more anterior cervical centra fused.	16. Neck region short, but anterior cervical centra all separated by wide intervertebral spaces.
17. All discrete cervical and caudal intercentra apparently lost in some late forms, elements of lower arches not united ventrally.	17. Cervical intercentra few and small. Caudal intercentra large and united ventrally to form Y-shaped lower arches.
18. Zygapophysial facets of vertebrae reduced or brought into one plane and united.	18. Zygapophysial faces in the anterior half of the vertebral column neither united nor brought into the same plane.
19. Neural spines of vertebrae strongly flattened laterally.	19. Neural spines averaging relatively thick, and may be circular in cross-section in the anterior half of the vertebral column.
20. Posterior region of tail bent downward sharply for support of lower lobe of fluke.	20. Distal region of tail showing relatively less marked downward curvature. Sometimes bent upward strongly, and then downward.
21. Neural arches of caudal region reduced near bend of tail, owing to change of form of fluke.	21. Neural arches in middle third of caudal region not reduced. In some cases the arches in this region are much elongated and erected to broaden this region of the tail.
22. Scapula narrowed distally.	22. Scapula expanded distally.
23. Episternum T-shaped instead of deltoid.	23. Episternum approaching a deltoid rather than T-shaped form where known *(Mixosaurus)*.
24. Abdominal ribs often not united along median line.	24. Abdominal ribs heavy, and united in a prominent spine on the median line.

It will be noted that in the extended series of differences which appear in the table above, nearly all are features of the skeleton which have been considered as standing in close relationship to aquatic adaptation. These include also the principal ordinal characteristics distinguishing the group. The last three characters only are not considered as necessarily standing in close relation to aquatic adaptation, but possibly even these are to be ascribed to the effect of adaptation of this nature. In the contrast between the earlier and the later ichthyosaurians it is seen that nearly all of the characters of the later forms which are considered as standing in close relationship to aquatic adaptation are less distinctly expressed in the Triassic representatives of the group. In other words the characteristics of the earlier forms are practically all nearer those of shore or land reptiles, and those of the later ones take the direction of specialization toward an adapted fish-like form. The evidence before us shows that the trend of the specialization of the Ichthyosauria has been to develop those features which are of importance in purely aquatic life, and to reduce in importance those structures which have little or no function in such an environment as would be met under aquatic conditions.

In the earlier stages of the study of the Ichthyosauria various opinions were expressed[28] as to whether the characters showing close relation of these forms to their aquatic environment were survivals from a very primitive fish-like ancestral type, or whether they were secondarily acquired through accommodation of a land type to life in the sea. Practically all investigators who have expressed themselves on this point in recent years have held to the opinion first given a basis of observed fact by Baur (1887, 1), *viz.*, that the ichthyosaurs are specialized aquatic forms occupying in the Reptilia a position similar to that of the cetaceans in the Mammalia. This view receives support amounting to a demonstration from the evidence gathered in a study of the history of the group. Not only is the stage of evolution of the Triassic representatives nearer the shore or semi-aquatic reptilian type than in the later ones, but a definite and fairly regular gradation or progressive specialization from the earliest forms to the latest seems to be recognizable in many parts of the skeleton. The evidence of gradual modification toward the fish-like type presents itself not only in a comparison of the types of the successive periods with each other, but it is almost as distinctly seen in contrasting the forms of the latest Triassic with those from the middle division or from the lower part of the Upper Trias. It is clearly noticeable again in contrasting the faunas of the Upper and Lower Lias, or in a comparison of the Upper Liassic species with those of the later Jurassic and Cretaceous. Taken as a whole the evidence is of such a nature as to leave no room for doubt as to the course of evolution of the known representatives of the Ichthyosauria. While we are unfortunately not able to see back to the beginning of the evolutionary history, extending from the Middle Trias to Cretaceous, it can hardly lead from any other than a typical reptile with extremities constructed largely, if not entirely, for ambulation.

In the evolutionary series beginning with the unknown crawling ancestor of the ichthyosaur, Middle Triassic forms of the type of *Cymbospondylus* represent a stage in which the animals had already abandoned the shore as a place of regular habitation, but still retained in their skeletal structure enough original characteristics to give a clue to their origin. Contrasted with the Middle Triassic *Cymbospondylus* type we have at the latter end of the series such forms as the *Baptanodon-Opthalmosaurus* group in which the adaptation to life in deep water is so extreme as to have suggested to otherwise careful investigators that these forms were less specialized than any other reptiles.

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[28] Gegenbaur, C., Untersuchungen zur vergleichenden Anatomie der Wirbelthiere. 2 Heft., 1865. Paddles derived from selachian fins.

Haeckel, E., Generelle Morphologie der Organismen. Bd. 2, p. 134, 1866. Resemblance to fish secondarily acquired.

ORIGIN OF ICHTHYOSAURIA.

Though the ichthyosaurs were throughout their whole known history constantly specializing along the line of adaptation to their aquatic environment, we find that as early as the Middle Triassic they were already in the class of the highly specialized aquatic reptilian types. From what we know, we can hardly suppose them to have separated themselves from the parent shore type far enough to be called ichthyosaurs later than the early part of the Trias. Possibly their origin dates from an even earlier period. There seems, therefore to be good reason for considering them one of the oldest of the reptilian orders. The primitive ichthyosaur was evidently a typical reptile, and considering the necessarily early period of its origin, antedating as it does that of most of the other orders, it may be derived only from one of the very primitive members of this class. Unless we consider the ichthyosaurs as themselves one of the primitive divisions of the Reptilia, we have only the most primitive representatives of the cotylosaurian, synapsidan and diapsidan stems with which it may stand in the relation of descent.

Woodward[29] has included the ichthyosaurs in the reptilian group in which the skull possesses a single temporal arcade, along with the Anomondontia, Sauropterygia and Chelonia; at the same time calling attention to the very primitive characters of the skull. Cope[30] in one of his last phylogenic arrangements of the reptilian orders, derived the Ichthyosauria directly from the primitive Cotylosauria.

Broom[31] has separated the ichthyosaurs from both the Synapsidan and Diapsidan groups. More recently Williston[32] has called attention to the fact that "the presence of an original lateral temporal opening is by no means proved." Baur[33] considered the ichthyosaurs rhynchocephalian. McGregor[34] and Osborn[35] have suggested close relationship of the Ichthyosauria with the Rhynchocephalia.

Excepting in those characters indicating adaptation to aquatic environment the ichthyosaurian skeleton is undoubtedly very primitive. Whether it has been diaptosaurian, synapsidan or cotylosaurian in its original form is less certain.

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[29] Woodward, A. Smith, Vertebrate Palaeontology, p. 143, 1898.

[30] Cope, E. D., Primary Factors of Organic Evolution, p. 115, 1896.

[31] Broom, R., Proc. Zool. Soc. Lond., 1901.

[32] Williston, S. W., Biological Bulletin, vol. 7, p. 186, Sept. 1904.

[33] Baur, G., Am. Nat., vol. 21, p. 837, 1887.

[34] McGregor, J. H., Science N. S., vol. 16, p. 27, July 4, 1902. Also, Mem. Amer. Nat. Hist., vol. 9, part 2, p. 91, Feb. 1906.

[35] Osborn, H. F., Mem. Amer. Mus. Nat. Hist., vol. 1, No. 8, p. 456, Nov. 1903.

Some of the most definite opinions regarding relationship to other groups are those of the several writers who have considered the Rhynchocephalia the ancestral type. While the Ichthyosauria show a strong resemblance to these diaptosaurians in many characters, it is to be questioned whether this similarity is more than a survival of common primitive characters in both. At any rate, if it be shown that a number of the most characteristic features of the Diaptosauria are lacking in the Ichthyosauria we shall hardly be justified in considering the diaptosaurs as their ancestors.

Recently McGregor[36] has expressed the opinion that the diapsidan order Phytosauria includes the nearest known relatives of the ichthyosaurs, and that they represent the nearest approximation to the amphibious form through which the ichthyosaurs passed in their evolution from rhynchocephalian-like ancestors, "though no *known* phytosaurian can actually be the ancestor of the Ichthyopterygia."

The phytosaurs and the ichthyosaurs have many characters in common, and particularly the phytosaurs show some affinity with the most primitive diaptosaurians. There are, however, a number of characters which seem to indicate that the phytosaurs and ichthyosaurs have arisen quite independent of each other. In order also to have the appearance of being intermediate between the ichthyosaurs and the primitive diaptosaurs, the phytosaurs should precede the ichthyosaurs in time. We find, however, that the phytosaurs belong mainly to the latter part of the Upper Triassic, while the ichthyosaurs were a sharply differentiated and highly specialized group early in Middle Triassic time, and had already expressed in them most of the characters which separate their Jurassic representatives from the phytosaurs. In spite of the fact that the orbits were much smaller in the earlier ichthyosaurs than in the later genera, and that the inferior temporal arcade was large enough so that a primitive lateral opening would not necessarily be closed by contraction of the bar, this lateral opening is not present as in the Phytosauria. There are also no antorbital and no external mandibular vacuities in the ichthyosaurs; the squamosal and supratemporal are not fused; the pleurocentrum of the atlas was large; no ectopterygoid is certainly known; a large pineal foramen was present; the exoccipital and opisthotic were not fused; there was no tendency to develop a secondary palate; the pterygoids were in contact with the basioccipital; and the thoraco-lumbar vertebrae were more numerous than in the phytosaurs.

The phytosaurs are typically rhynchocephalian in more characters than the ichthyosaurs. The main features in which they show special similarity to the ichthyosaurs are found in the structure of the rostrum and the nasal region. The median position of the nares appears, however, almost a normal character of marine air-breathing vertebrates, and the extension of the premaxillary re-

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[36] McGregor, J. H., Op. cit., p. 89.

gion occurs in the development of an elongated snout in most groups of reptiles excepting the Crocodilia and Choristodera; so that in the case of the Phytosauria the peculiar feature is the presence of an elongated snout with median nares in a fresh-water form not otherwise highly specialized. The significance of this parallelism is possibly no more than that the phytosaurs are not necessarily crocodilian, rather than that the ichthyosaurs are modified phytosaurs.

It seems that the characters in which the phytosaurs and ichthyosaurs differ at least balance the special resemblances which may be common inheritances from very early ancestors. It also appears easily possible that the time of origin of the ichthyosaurs was at so early a date that some diaptosaurian characters, as the lateral temporal opening, have never appeared in them. The phytosaurs are not far removed from the typical Diaptosauria. They may have originated early or may have had their origin in the latter part of Middle Triassic time. It is doubtful whether their peculiarities, aside from very primitive features which parallel characters in the ichthyosaurs, existed in the phytosaurs as early as the time of origin of the Ichthyosauria. It is not improbable that the phytosaurs simply parallel to some extent the amphibious type through which the ichthyosaurs must have passed in their evolution, and that they developed as a distinct phytosaurian group after the ichthyosaurs had become typical marine animals.

VARIATION IN THE ICHTHYOSAURIA.

The Ichthyosauria exhibit through the whole range of the order such a constancy in the major features of their skeletal plan that no question has ever arisen as to whether a particular form is properly considered as a member of the group. There is, however, a considerable range of variation in certain important groups of characters, and indefiniteness rather than fixity of generic and specific features seems to be the rule in the better known forms. Though the variability is shown to some extent in all parts of the skeleton it appears in its most extreme form in those structures which are most distinctly modified in adaptation to aquatic life.

An example is seen in the paddles of *Ichthyosaurus,* the fundamental structure of which has always remained much the same. In the podial region the digits have always held close together, in contrast to the divergent fingers of the mosasaurian type; and the phalanges have increased greatly in number, with accompanying average shortening. The number of digits has however varied between *Ichthyosaurus communis* with a possible ten longitudinal rows of phalanges, and *I. acutirostris* with three, or *Shastasaurus* probably with two and a rudimentary third. With the variation in the number of digits, the number of the phalanges and the form of the paddle have generally varied, so that the many fingered paddle of *I. communis* is broad but short, and the paddles of *I. acutirostris* are excessively long and slender. The two types of paddles represented by *I. communis* on the one hand, and *I. platyodon* with *I. acutirostris* on the other hand, distinguish two groups of ichthyosaurs which are in the main fairly distinct (figs. 103 and 104). They were separated by Kiprijanoff[37] as Latipinnipedes typified by *I. communis,* and Longipinnipedes represented by *I. platyodon;* but were not designated as genera, as there seemed to be no point at which a dividing line could be drawn satisfactorily. This classification was accepted in somewhat modified form, by Lydekker[38] in preparing his catalogue of fossil reptiles of the British Museum, the group names being changed to Latipinnati and Longipinnati. The groups have been recognized by Fraas and other investigators who have made particularly close studies of the structure and relationships of the Ichthyosauria. Fraas accepted the divisions Longipinnati and Latipinnati but treated them as groups, and not genera, as had been done by Kiprijanoff and Lydekker. More recently they have been designated as distinct genera by Jaekel[39] and Boulenger.[40]

If the longipinnate and latipinnate divisions of the ichthyosaurs of the Lower Lias actually represent distinct groups of species tending to specialize in somewhat different directions, they should be recognized as separate genera. It is, however, true that most of the investigators who have worked over large collections have found the separation of the two divisions so difficult that they have refrained from giving generic values to them.

To a considerable extent the same difficulties that are met in this grouping of Jurassic species of the true ichthyosaurs are found in the definition of other genera and species. The species of *Opthalmosaurus* and *Baptanodon* appear quite widely separated from the typical forms, but in reality most of the characters which separate them from *Ichthyosaurus* are to be found in various forms of *Ichthyosaurus* itself.

The statements which have been made regarding variation in the structure of the paddles might apply almost as well to most other portions of the skeleton in which characters of generic or specific rank appear, as in the facial region of the skull, the dentition, and the caudal fin. A general study of the considerable variations occurring inside the Ichthyosauria seems to show fewer interruptions between the various forms recognized than commonly appear in natural groups. These facts apparently indicate a high degree of plasticity

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[37] Kiprijanoff, M., Mem. l'acad. imp. d. sc. St. Petersburg, VII ser., t. 28, no. 8, p. 88.

[38] Lydekker, R., Geol. Mag. London, 1888, Dec. 3, vol. 5, p. 310. Also Catlg. Foss. Rept. and Amphib. Brit. Mus., pt. 2, p. 13, 1889.

[39] Jaekel, O., März-Protokoll d. Deutsch, geol. Gesel., Bd. 56, Jahrgang, 1904, p. 32. Jaekel proposed the name *Eurypterygius* for the latipinnates, and *Stenopterygius* for the longipinnates.

[40] Boulenger, G. A., Proc. Zool. Soc. Lond., vol. 1, p. 425. Aug. 2, 1904. Boulenger uses the generic name *Ichthyosaurus, sensu stricto,* for the Latipinnati; and *Proteosaurus* Home for the Longipinnati.

in the ichthyosaurian types of Jurassic time. Judging from the number of forms known in the Trias this plasticity was at least as pronounced in that period.

The plasticity, or the greatest variation, in ichthyosaurs has appeared in those portions of the skeletal structure which stood in the most immediate relation to their environment, and could be most easily modified by changes in habits, food, or any variation in the elements of their surroundings. The most variable portions of the skeleton are probably the paddles and the caudal fin. In many of the principal characters of the cranial region of the skull a most remarkable conservatism is shown; only in the form of the rostrum and in the nature of the orbit do we find variation comparable to that of the limbs. The significance of the location of the centers of greatest variation seems to be that the variation is to a great extent determined by the peculiar relation of the animal to its environment, and in those centers where no distinctly important relation of this nature exists variation has been insignificant.

The fact that the different ichthyosaurian forms recognized are not easily separable, offers some support to the view that they represent stages in a differentiation of the group which has taken place at a fairly uniform rate, and has not therefore given us sharply distinguished and persistent resting stages, such as have sometimes been considered to represent genera and species.

In so far as the above suggestions hold good, the evolution of these forms may indicate that the species have originated either as the direct result of use and disuse due to pressure of the environment; or that they have arisen as variants or mutants in which the direction of mutation has been determined by the same external factors which would be supposed to direct use and disuse in the application of the Lamarckian hypothesis. According to this suggestion the known ichthyosaurian types may be explained as having arisen under slightly different sets of conditions, either at the same time in different places, or at different times in the same place.

Whatever be the ultimate cause of the progressive specialization seen in the Ichthyosauria, this tendency became almost a constitutional feature. In spite of minor variations and of the inclination of geographically separated types to take somewhat different paths in their specialization, the general trend of evolution of all forms over the earth has been in the same direction, and at about the same rate. In most instances the horizon in which a Triassic ichthyosaur belongs may be determined by the degree of specialization of any one of a considerable number of structures, as *e.g.*, the zygapophyses of the vertebrae. Where characters of late forms seem to appear in early ones, the average of the characters of the whole organism will be found to indicate a relatively low level of specialization. In the tail of the Middle Triassic *Cymbospondylus* the reduced upper arches of the distal caudal region suggest a caudal series like that of the later

Ichthyosaurus, but the vertebral centra of this region in *Cymbospondylus* offset the beginning specialization of the arches by preserving a remarkably high and compressed or primitive form.

The tendency which the Ichthyosauria have shown to keep the same general trend of specialization through their whole history, and in all geographic regions, is not contrary to the suggestion advanced above; *viz.,* that the modifications introduced in this group usually indicate the bringing about of a closer relation to their environment. The all important feature which distinguishes the Ichthyosauria as an order is their aquatic adaptation. Entering as they have into a realm very different from that in which the immediately ancestral types have lived, the factor which has overshadowed all others has been the necessity of getting a working basis for life in water, particularly with relation to locomotion. The extent of the changes required in the accommodation of all ichthyosaurians, whenever and wherever they have existed, to those simpler features of aquatic life which are the same in all periods and in all places, may be responsible in a large measure for the generally similar trend of evolution.

In this connection we naturally enquire why it was necessary for the Ichthyosauria to leave their original environment, for surroundings in which an entirely different equipment was necessary. The only explanation which offers itself suggests a possible change of food habits, through the discovery that certain of the thriving cephalopod groups of the early Mesozoic furnished an abundant and easily obtained food supply. Even in the most favorable light, however, the problem of definite variation in the Ichthyosauria in some of its aspects seems to invite a resort to orthogenesis; or to the view that there are factors influencing variation which are not as yet understood, and that these tendencies to similar variation may express themselves in related groups for long periods, and in regions widely separated geographically.

Taking the history of the Ichthyosauria from the earliest stages to the latest, the following statements regarding the group seem to be warranted by the known succession of forms: (1) The group is unquestionably a unit, and no doubt has arisen as to the common origin of the forms included in it. (2) There has been a very considerable advance in specialization extending through a long period. (3) Variation has been greatest in those structures standing in the closest relation to aquatic adaptation. (4) Variation seems generally to be of the continuous rather than of the saltatory type. (5) Variation is remarkably direct, or takes much the same course in all forms of the same geological age.

CLASSIFICATION OF THE ICHTHYOSAURIA.

After some knowledge had been obtained of types distinct from *Ichthyosaurus,* the earliest attempt at classification of the groups included in the Ichthyosauria, was that of Baur (1887, 1), in which three families, the Ichthyosauridae, Baptanodontidae, and Mixosauridae, were established. To these Merriam has more recently added a fourth group, the Shastasauridae (1902, 2). At the time when these families were described the arrangement of the ichthyosaurian forms seemed fairly simple, but in reality comparatively little was known regarding any of these groups excepting the Ichthyosauridae. Since that time the principal points in the structure of *Mixosaurus* have been made known by Repossi (1902), the material available for study of the American Triassic forms has very greatly increased, and large additions have been made to our knowledge of the structure of *Baptanodon*[41] and *Opthalmosaurus.*[42]

With the recent increase in the available information, many points of relationship have been determined among the ichthyosaurian forms, but the tendency on the whole has been to make a satisfactory arrangement more difficult than before. While the four families already described may still be recognized as fairly distinct groups, they do not adapt themselves to a phylogenic scheme such as would seem to be demanded by the long historic series now known, and in which cognizance is taken of the facts of geographic distribution. The evolutionary history of the Ichthyosauria now extends from the Middle Triassic to the Cretaceous, a considerable series of forms being known from all of the principal marine horizons representing this division of geologic time. We find the Ichthyosauria as a group showing a remarkable unity with a fairly direct tendency of evolution marked out in all the subdivisions, and a considerable number of stages are passed through in the known history. It is therefore to be expected that to express the classification of the group in the form of phylogeny would be a fairly simple matter. In a general way the horizontal classification, *viz.,* that recognizing the forms of only one horizon, meets few obstacles. In a linear arrangement the tendency of progression, specialization, or evolution is distinct, and the stages recorded are fairly definite. In viewing the whole scheme both horizontal and linear it is, however, difficult to discover characters which are fundamental and persistent, or which are adaptive and persist unchanged to such a degree that they may be used in a classification scheme. To a certain extent it is true that in passing from one period to another the characters considered as diagnostic are replaced by others.

The characters on which the classification of the Ichthyosauria was based by Baur included only modifications of the extremities and dentition, both of them features which would most readily respond in adaptation to aquatic conditions. The distinguishing characters of the Shastasauridae as originally described were found in the "peculiar articulation of the dorsal ribs, the form of the pelvic arch, and the presence of the long-spined chevrons." It has been

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[41] Gilmore, C. W., Mem. Carneg. Mus., vol. 2, no. 2, and no. 9.

[42] Andrews, C. W., Geol. Mag., Dec. 5, vol. 4, p. 202.

shown more recently that the type of limb structure in *Shastasaurus* is also quite different from that in the other divisions of the Ichthyosauria.

Of the various groups of characters in which the Ichthyosauria show differences, the strongest contrasts are found in the (1) limbs, (2) pelvic arch, (3) caudal fin, (4) caudal chevrons, (5) articulation of dorsal ribs, and (6) the dentition. The variation in most of these characters may apparently be attributed to adaptation of the peculiar type expressed in the Ichthyosauria.

If the ichthyosaurs be taken as a whole, one of the most striking contrasts is shown in a comparison of the Triassic and post-Triassic forms, particularly in the characters just mentioned, as is indicated by the following table:

	TRIASSIC						JURASSIC CRETACEOUS		
	Cymbospondylus	*Mixosaurus*	*Merriamia*	*Delphinosaurus*	*Shastasaurus*	*Toretocnemus*	*Ichthyosaurus*	*Baptanodon*	*Opthalmosaurus*
Rib articulation mainly single	x	x	x	x	x				
Rib articulation mainly double						x	x	x	x
Distal end of caudal series strongly decurved			?		?	?	x	x	?
Caudal vertebrae with Y-shaped lower arches	x	x	?	x	x	x			
Pelvis plate-like, not reduced	x	x	?	x	x	x			
Pelvis much reduced							x	x	x
Scapula much broadened distally	x	x	x	x	x	?			
Epipodials separate and relatively long	x	x	x	x	x*	x			
Hyperphalangy developed							x	x	
Phalangeal elements sometimes shafted	?	x	x	?		x			
Phalanges polygonal or discoidal	?			?	x		x	x	x
Phalanges reaching double the normal formula for diapsidan reptiles	?			?	?		x	?	
Teeth numerous	x		x	?	?	?	x		
Teeth differentiated		x		?	?	?			
Teeth in pits	x*	x		?	?	?			

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* In part.

Considered without regard to age, the dividing line in the Ichthyosauria would certainly be drawn between the well-known Triassic genera on the one hand, and on the other hand the post-Triassic *Ichthyosaurus* and later types. Considered from the historical point of view it might be presumed that as most of the characters in which these groups differ are closely connected with the peculiar kind of adaptation which we see here, the differences simply express stage of evolution; and that probably some of the known Triassic forms are ancestral to *Ichthyosaurs, Baptanodon,* and *Opthalmosaurus.*

If the post-Triassic types be excluded from consideration, as presumably derived from some of the known Triassic forms, the contrasts shown in the remaining ichthyosaurs are much less marked. The principal contrasts seen in the Triassic forms are in the structure of the podial region of the limbs, in the rib articulation of the cervical and dorsal region, and possibly in the dentition. In *Mixosaurus* the podial region is broad and forms a relatively large part of the paddle. In the American Upper Triassic genera, which are probably slightly younger than *Mixosaurus,* the corresponding region forms a relatively small portion of the limb. It is also relatively narrow and the number of digits is reduced. In *Cymbospondylus,* from an earlier Middle Triassic stage than *Mixosaurus,* the structure of this region is not certainly known, but the podial portion appears to have three transverse rows of phalanges like *Merriamia,* while the form of the distal end of the ulna suggests the presence of a fourth or posterior element in the proximal row of the mesopodial region as in *Mixosaurus.* In the rib articulation, *Mixosaurus* seems to be characterized by the presence of only a single head in the dorsal and cervical region, and a possible incipient division of the broad heads of the posterior dorsals and anterior caudals. In all of the American Triassic genera, excepting *Toretocnemus,* no division occurs in any part of the series excepting in the the most anterior portion of the vertebral column, where it is always present. In *Toretocnemus* the middle dorsals show a wide division of the rib head. This seems to extend well back toward the pelvis. The anterior dorsal and cervical regions of this genus are unknown. The limb structure is apparently like that in *Merriamia.* In the specimens referred to *Mixosaurus*(?) *atavus,* the oldest known ichthyosaurian occurring in the Middle Trias, both single and double articulations occur, and two distinct types may be represented.

On the basis of difference of limb structure and rib articulation, *Mixosaurus* would apparently be separated from all of the American genera as a broad-paddled, pentadactyl type, in which bicipital rib articulation is reduced to a minimum. The American genera including *Toretocnemus* would be distinguished as narrow-paddled and with persistent bicipital rib articulation in the cervical region. *Toretocnemus* might be classed with the American shastasaurines as a form in which the limb structure had become narrowed or leptocheirous, but in which an original bicipital rib articulation had persisted. The European *M.*(?) *atavus* may be in part related to *Mixosaurus*, and in part to other groups with bicipital rib articulation.

It is doubtful whether any single group of characters should be used in attempting to determine the course of development or the relationships of the forms in this order. We may, however, fix upon those features which have been most persistent, and have generally followed the most direct course of evolution. The most persistently differing characters in close relation to adaptation are found in the variation in structure, and possibly in function of the paddles. This variation is apparent from the Triassic forms up to the acme of the Jurassic representatives of the group. The most marked difference in characters which might be considered as fundamental is found in the rib articulation. Both the broad and narrow types of paddles are far removed from a primitive form of the limb. While the rib articulation has evidently also varied considerably in all of the forms, it is to be presumed that in certain parts of the vertebral column the characters have changed less than in the limbs, which are in closer touch with the environment.

If an attempt be made to classify all of the ichthyosaurian groups on the basis of the structure of the paddles or of the rib articulation, it is seen that the characters do not vary together. They are so entangled that broad and narrow types of paddles appear in forms with mainly bicipital articulation, as in the latipinnate and longipinnate forms of *Ichthyosaurus,* and are also found in types with mainly single articulation as in the broad-paddled *Mixosaurus* and the narrow-paddled *Merriamia.* If therefore any phylogenic scheme is to be based on these characters, it will be necessary to determine which of these two kinds of variation is the more primitive, and which has developed secondarily in the separate lines of descent. Of the two sets of characters, the nature of the rib articulation would seem to be more nearly fundamental than the structure of the paddles; and one of the forms of rib articulation is presumably primitive, the other being a variation from it.

From evidence which has been presented in the general discussion of the vertebrae (p. 53) there seem to be some reasons for considering the double articulation as more probably primitive than the single articulation. If such be the case, all Triassic forms excepting *Toretocnemus* and *M.*(?) *atavus* must be set aside as specialized and not ancestral to *Ichthyosaurus.* If the double articulation be primitive, the forms with bicipital articulation, as *Ichthyosaurus* and *Baptanodon,* have retained a primitive character not preserved in the shastasaurines or in *Mixosaurus,* and these groups must be considered as specialized branches from the persistent stock, and not ancestral to *Ichthyosaurus.*

On the other hand, if the single articulation of the rib head be primitive, *Mixosaurus* may lead directly toward *Ichthyosaurus,* though the American forms would still remain as a separate group, excepting possibly *Toretocnemus.* This last genus, in spite of the presence of what is considered a primitive character, is geographically so situated as to make its relationship to *Ichthyosaurus* very doubtful, and the similarity of its limb structure to that of *Merriamia* makes it probable that it is to be considered as a persistently primitive form coming from the same stock as *Merriamia.*

If the double rib articulation be primitive, there is as yet no form known which would be considered as the ancestral ichthyosaurian type, unless it be one of the imperfectly known forms of *M.* (?) *atavus* of Europe. If for no other reason, the geographic situation of this type, which is itself a factor in classification, is such as to suggest that *Ichthyosaurus* is descended from it, and that *Mixosaurus* is also derived from it. Whether the American genera can be considered as derived from *M.* (?) *atavus* or from some earlier form must be left undetermined until more is known of *M.* (?) *atavus.* As yet the available material is very scanty. The geographic situation of *M.* (?) *atavus* is also very distant from that of the oldest American Middle Triassic forms, and the disparity in age is not great; so that the ancestors of the American forms may have come from some region other than Europe.

Without being able to construct a thoroughly satisfactory phylogenic scheme, there appears to be good reason for considering that there are present in the known material representing this order, at least four groups in which the common origin of the constituent members is fairly certain, and in which the rank of the larger included groups is high enough so that the four divisions must themselves be considered as not ranking lower than subfamilies. These divisions are the Ichthyosauridae, Baptanodontidae, and Mixosauridae of Baur, and the Shastasauridae of Merriam. Of these groups the Ichthyosauridae and Baptanodontidae are both types with bicipital articulation of the dorsal ribs. They are otherwise closely related, and may be brought together as one group, which might well be designated the Ichthyosauridae with two divisions. If *Ichthyosaurus* is divided into several genera as is the present tendency of writers, and if *Baptanodon* is to be distinguished generically from *Opthalmosaurus,* this family should be subdivided into two subfamilies, the Ichthyosaurinae and Baptanodontinae.

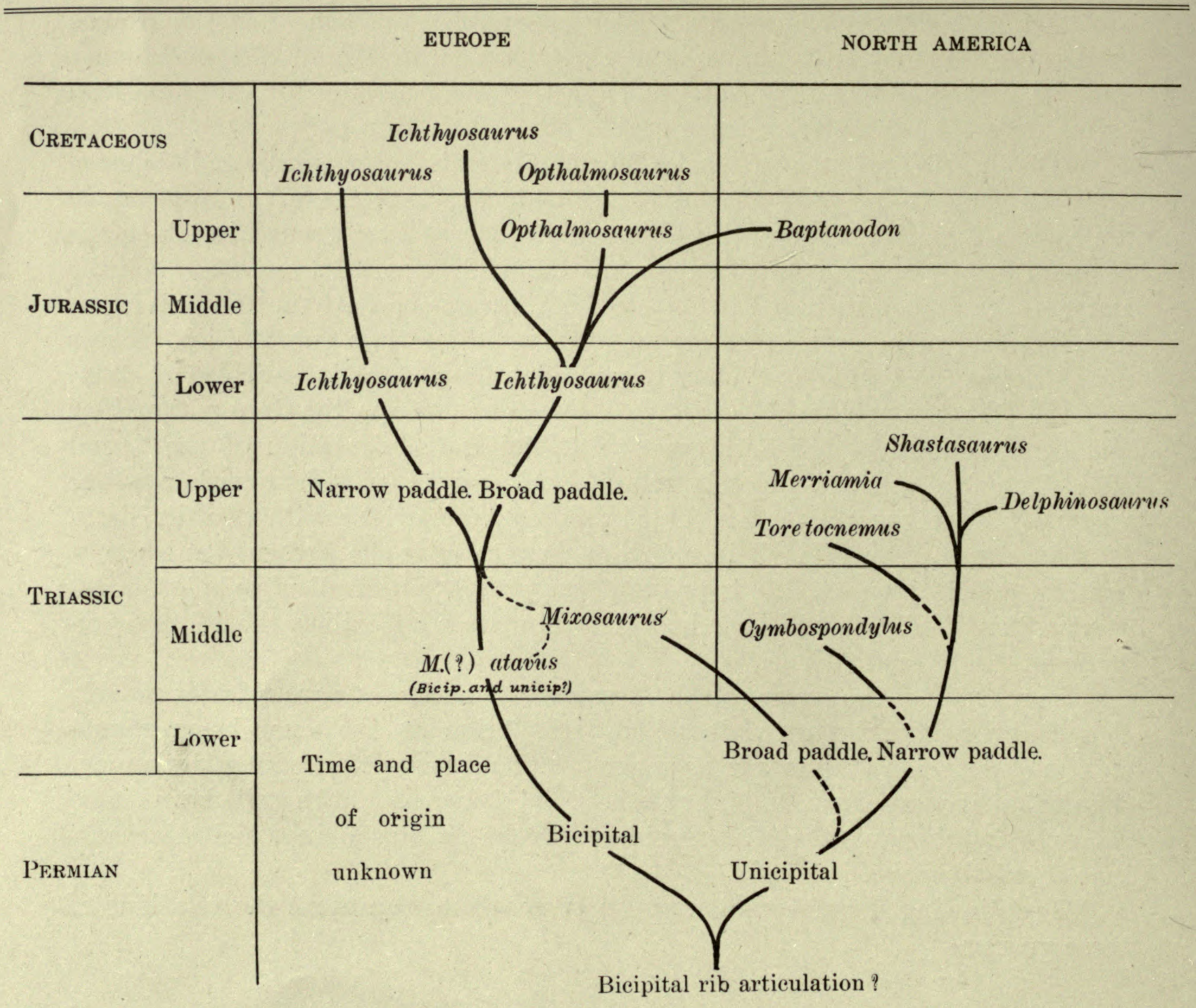
The relation of the American shastasaurs to the mixosaur group is not entirely clear, but the character of the dorsal rib articulation and the general correspondence in other parts of the skeleton suggest that the resemblance may mean more than primitiveness alone, and that these two divisions should be united in a larger group of family rank, the Mixosauridae with the Shastasaurinae and Mixosaurinae as subdivisions.

The following arrangement seems most nearly to represent the relations of these groups:

Ichthyosauria

- Mixosauridae
  - Mixosaurinae
    - *Mixosaurus*
  - Shastasaurinae
    - *Cymbospondylus*
    - *Merriamia*
    - *?Toretocnemus*
    - *Delphinosaurus*
    - *Shastasaurus*
- Ichthyosauridae
  - Ichthyosaurinae
    - *Ichthyosaurus*
  - Baptanodontinae
    - *Baptanodon*
    - *Opthalmosaurus*

In this arrangement *Toretocnemus* is placed with the Shastasaurinae as a type in which the rib articulation has remained more primitive than in the others, or has been secondarily divided in the posterior dorsal region. *M.* (?)



atavus may be associated with either of the two families; it may be subdivided into two quite distinct groups and associated with both; or it may be considered ancestral to both.

The phylogenetic scheme on the preceding page illustrates the broader relationships of the ichthyosaur groups, as they may be assumed to be situated on the basis of a primitive bicipital rib articulation.

The major divisions of the Ichthyosauria may be defined as follows:

ICHTHYOSAURIA.

MIXOSAURIDAE.

Articulation of dorsal ribs generally unicipital. Hypocentral elements of the caudal region uniting to form long-spined chevrons. Distal region of caudal series not strongly decurved. Zygapophyses in anterior half of vertebral column consisting of distinctly separated lateral faces. Number of presacral vertebrae may reach 65. Pelvic elements plate-like, relatively large. Scapula expanded distally. Epipodial elements relatively elongated, and separated by a cleft (excepting in *Shastasaurus careyi*). Hyperdactyly not developed. Hyperphalangy less marked than in Ichthyosauridae. Phalangeal elements frequently elongated and shafted. Facial region shorter and maxillary longer than in Ichthyosauridae. Orbits relatively small in most forms. Postorbital bar not markedly narrowed. Teeth few to numerous, isodont or differentiated, in open grooves or in pits.

Mixosaurinae. Presacral vertebrae 48-50 (?). Cervicals with unicipital rib articulation (?). Distal region of caudal series curved upward anterior to the posterior end, and slightly decurved distally; neural spines elongated and erected in the region of curvature. Pubis without obturator notch or foramen. Interclavicle with expanded median stem. Podial portion of paddles relatively long and broad, five digits present. Orbits moderately large. Teeth well spaced, set mainly in pits, differentiated.

Shastasaurinae. Presacral vertebrae 45 (?) to 65. Cervicals with bicipital rib articulation. Distal region of caudal series as in the Mixosaurinae, or somewhat decurved as in the Ichthyosauridae. Pubis with obturator notch or foramen. Paddles with relatively short and narrow podial region. Digits where known reduced to three or four. Orbits small to large. Postorbital bar not greatly narrowed. Teeth numerous, close set in open grooves or in pits.

ICHTHYOSAURIDAE.

Articulation of the presacral ribs mainly bicipital. Hypocentral elements of the caudal region sometimes absent, when present not meeting to form long-spined chevrons. Distal portion of caudal series sharply decurved and enclosed in the lower portion of a two-lobed sculling fin. Zygapophyses consisting of a single anterior or posterior face. Presacral vertebrae about 45 in number. Pelvic elements much reduced. Scapula narrow distally. Hind limbs generally much reduced. Epipodial elements very short and not separated by a cleft.[43] Hyperdactyly frequent. Hyperphalangy very pronounced. Phalangeal elements polygonal or rounded. Facial region relatively long. Maxillary relatively short. Orbits very large. Postorbital bar generally narrow. Teeth numerous, isodont, in open grooves.

Ichthyosaurinae. Hypocentral caudal elements usually present.[44] Inferior pelvic elements separate or fused. Epipodial region of anterior limbs including only two elements.[45] Epipodial bones angular in outline. Phalangeal elements polygonal, sometimes notched on the anterior side in the anterior row. Teeth numerous.

Baptanodontinae. Hypocentral elements reduced, or absent from caudal region. Ilium and ischium fused. Epipodial elements three in number in the anterior limb. All limb elements excepting the propodial and anterior epipodial are discoidal in form, and with excavated or pitted margins. Orbits very large, and postorbital bar very narrow. Teeth few and small.

SYSTEMATIC DESCRIPTIONS.

MIXOSAURUS(?) ATAVUS (Quenstedt).

Ichthyosaurus atavus Quenstedt. Petrefactenkunde, Aufl. I. 1852, p. 129; Aufl. II, 1867, p. 160, Taf. 6, fig. 7-10.

Mixosaurus atavus, major and *minor* (Fraas). Ichthyosaurier d. Süddeutschen Trias- and Jura- Ablagerungen, 1891, p. 37, Taf. 1, fig. 17 and 18; Taf. 3, fig. 1-16.

Ichthyosaurus(?) atavus (Merriam). Am. Jour. Sc., vol. 19, p. 30. Jan., 1905.

To this species Quenstedt referred a number of fragmentary Triassic specimens evidently representing ichthyosaurians. In the absence of distinguishing characters it was included in the genus *Ichthyosaurus.* In additional material of similar type Fraas recognized characters separating this form from *Ichthyosaurus,* and included it in the genus *Mixosaurus,* which had been described by G. Baur from a study of the Italian Triassic material. More recently Merriam has questioned the generic identity of this form with the species referred to *Mixosaurus.*

Vertebral Column.—The vertebrae of this form are known through a comparatively few specimens, nearly all of which are represented by centra without arches.

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[43] Very exceptionally slightly separated.

[44] See page 46.

[45] Rarely, as in *Ichthyosaurus extremus,* with more than one element.

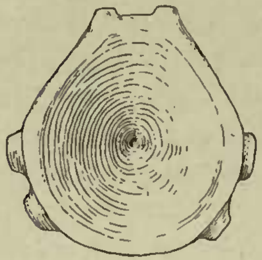
In the collection of the Königlichen Naturalien-Cabinet of Stuttgart there is a small centrum which, as far as can be determined, agrees in all its characters with the most anterior dorsal or cervical centra of *Ichthyosaurus* or *Cymbospondylus*. It is somewhat broader than high, and apparently had two lateral facets for rib articulation (fig. 61). The upper portion of the vertebra is however damaged so that the complete separation of the facets cannot now be proved. The upper facet was evidently continuous with the superior surface for articulation with the neural arch. A somewhat broken centrum, no. 3068, in the collection of the Polytechnikum of Zürich seems also to belong in this region, as the superior articulation with the rib is continuous with the articular surface for the upper arch. Part of the lateral face of the vertebra was unfortunately covered with matrix. This centrum is nearly circular in cross-section. The one from the Stuttgart collection has nearly the same form, but is a little broader, indicating probably a position near the posterior end of the cervical region.

There are no vertebrae available which represent the middle dorsal region, unless possibly a specimen (fig. 62) figured by Fraas (1891, Taf. 3, fig. 12) belongs there. This last vertebra is a very little higher than wide and seems to bear a single small apophysis just above the middle. The writer has not seen so small an apophysis for unicipital articulation of dorsal ribs in any ichthyosaur, but apophyses for rib articulation, of this size and similarly situated on the side of the centrum, are found in the middle tail region. The width of the centrum is, however, greater than is generally seen in caudal centra of Triassic genera and the inferior surface seems to show no facets for chevrons. Fraas considered this centrum a caudal. If it is not a caudal, it might possibly be considered as an anterior dorsal in which the tubercle of a widely-forked rib head rested entirely on the base of the upper arch.

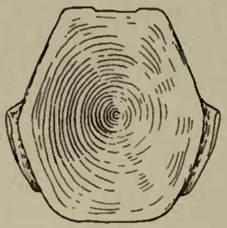
Several vertebrae differing considerably in their characters seem to represent the posterior portion of the dorsal region. Of these the larger number are like figures 63, p. 50; and 115*a* and 115*b*. The first of these two specimens was described by Fraas, the second is from the collection at Zürich. The form of the first centrum and the inferior position of the apophyses can probably indicate no other position in the column than that near the pelvic region. The inferior surface is rounded, showing no facets for hypocentra, and it is evidently not a caudal but a posterior dorsal. Other centra including one (figs. 116*a* and 116*b*) from the collections at Zürich, and two from the collections of the Technische Hochschule of Stuttgart show a form of the centrum somewhat similar to those just described, but support only a single lateral apophysis. There are in these specimens no distinct traces of facets for intercentra, and it is not probable that they were situated far behind the pelvic region.

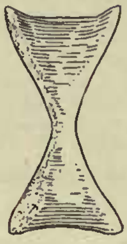
The first indication seems to be that the forms of centra discussed above


115a


115b


116a


116b


117a


117b


118


119


120a


120b


120c

Figs. 115*a* to 120*c*. *Mixosaurus* (?) *atavus* (Quenstedt). All figures natural size. Figures excepting 118 and 119 from rough sketches by the author.

Figs. 115*a* and 115*b*. Posterior dorsal vertebra showing double rib articulation. From the collections of the Polytechnikum, Zürich.

Figs. 116*a* and 116*b*. Posterior dorsal showing single rib articulation. From the collections of the Polytechnikum, Zürich.

Figs. 117*a* *and* 117*b*. Posterior dorsal showing double rib articulation. From the collections of the Polytechnikum, Zürich.

Figs. 118 and 119. Caudal vertebrae. (After Fraas.)

Figs. 120*a* to 120*c*. Anterior caudal vertebra showing facets for chevrons. From the collections of the Polytechnikum, Zürich.

show bicipital rib articulation in the dorsal region in one case and unicipital articulation in the other. That forms of articulation as different as these occurred in the same region of the vertebral column in variations of the same specific or even generic type seems improbable. It appears that we are dealing either with different parts of the vertebral column of similar individuals, or with quite different types occurring together, like *Toretocnemus* and *Merriamia* in the Upper Triassic of California.

With some evidence of double articulation in the anterior dorsal region and also in certain posterior dorsals, it is possible that all ribs back to the pelvis were double-headed, and that the vertebrae possessing a single large lateral apophysis, but without facets for lower arches, were in the pelvic region or immediately behind it.

If it should be shown that figure 62 page 50, really represents a type with unicipital middle dorsal ribs it is probable that there are two types represented, one with mainly or entirely single-headed ribs and the other with double-headed ribs back at least to the pelvis.

In neither case does there seem to be evidence that there are double rib articulations in the caudal region, behind vertebrae to which single-headed ribs are attached.

A typical vertebra from anterior portion of the caudal region is represented in figures 120*a,* 120*b,* and 120*c.* The centrum shows some lateral compression and has a hexagonal cross-section. The inferior surface presents prominent angles on which distinct facets for the inferior arches are present. Other posterior caudals, one of which shows a high degree of lateral compression, are represented by figures 118 and 119 (Fraas, 1891, Taf. 3, figs. 15*b* and 16*b*).

Most of the forms of vertebral centra seen in the specimens described above do not correspond exactly to those of other ichthyosaurians. In those with double-headed rib articulation the heads seem to have been more widely separated in the posterior dorsal region than in *Ichthyosaurus.* This may indicate a more primitive stage of a reptilian form originally with double-headed ribs, from which *Ichthyosaurus* is derived. The centra in which the position in the vertebral series has been determined by the form of the cross-section, and by the confluence of the upper portion of the rib articulation with that for the upper arch, are much like cervicals of *Ichthyosaurus, Shastasaurus,* or *Cymbospondylus.* In the centra with single articulation in the pelvic region the form is not very different from that in *Cymbospondylus.* If the specimen represented in figure 62, page 50, is a middle dorsal it is different from any other form known, but would apparently approach nearer to *Mixosaurus* than to any other genus.

As far as has been observed the centra of all of the vertebrae of the *M.*(?)

atavus type are deeply biconcave and do not show a marked flattening of the anterior and posterior faces near the periphery (figs. 117*a* and 117*b*). An exception may appear in some of the distal caudals.

Of the vertebral arches the only one known to the writer is the upper arch (figs. 34*a*-34*c*) described by Fraas (1891, Taf. 3, figs. 6*a-c*). This is an anterior dorsal arch of much the same type as in *Cymbospondylus*. The zygapophysial facets are very primitive in that they are still distinctly separated, they do not fall into the same plane, and they are still far from coming into a horizontal position.

Limb and Arch Elements.—The only limb bones of *M.*(?) *atavus* known, include a humerus described by Fraas (1891, Taf. 3, fig. 5), and several separated podial elements figured by Quenstedt (1852, Taf. 6, figs. 9-10). The humerus is a slender but not greatly elongated element with a very high pectoral ridge. Though somewhat damaged distally it does not appear to be more slender than the propodial element in a number of other ichthyosaurians (see von Huene 1902, p. 11). The other known limb elements are possibly mesopodials.

A number of bones from the arches are known but have not yet been described.

Jaws and Dentition.—Of the skull only a few fragments consisting of jaws are described. Excepting the somewhat greater prominence of the surface sculpture, and the insertion of the teeth these elements are much as in *Ichthyosaurus.*

The dentition which is fortunately known in several jaw fragments presents interesting characters which suggest that *Mixosaurus* is possibly a closely related type. In the several specimens which Fraas had before him there were present a portion of an anterior end of a jaw with slender conical teeth (fig. 15, p. 28) and a part of a jaw in which there are two teeth with low blunt crowns (fig. 16, p. 28). In one of the two teeth in the second fragment the crown is considerably compressed laterally, and is a little lower than in the other. In both teeth the crown shows surface markings on the enamel, and is apparently not reduced by wear. The bases exhibit strong folds of the dentine, and appear to be partly in pits. These specimens apparently indicate a differentiated dentition similar to that seen in *Mixosaurus*. The structure and insertion of these teeth are somewhat like that of the ichthyosaurians described from the Trias of Spitzbergen (see p. 149).

MIXOSAURUS Baur.

Ichthyosaurus (Bassani), Atti della Soc. Ital. di Sc. Nat., vol. 29, p. 15.
Mixosaurus Baur, Ber. d. 20 Versam. d. Oberh. Geol. Ver., 1887, p. 19.

Distal end of caudal region slightly bent but not sharply decurved as in *Ichthyosaurus,* broadened by elongation and erection of the vertebral arches.

Caudal vertebrae with Y-shaped chevrons. Rib articulation mainly single-headed, with a disposition to divide indistinctly shown in the posterior dorsal and anterior caudal regions. Inferior pelvic elements plate-like. Interclavicle tending to assume a triangular rather than a T-shaped form. Anterior limbs and arches considerably larger than posterior. Humerus not relatively elongated compared with *Ichthyosaurus,* in some instances much abbreviated or broadened. Epipodial elements relatively elongated, radius with median constriction, ulna convex on posterior border. Digits five, maximum number of phalanges ten to eleven in the longest digit. Phalanges generally somewhat elongated and with median constriction or lateral notch. Elements of posterior limbs generally less specialized than those of anterior limb. Skull relatively large compared with size of trunk. Facial region relatively short and maxillary relatively long compared with the form in *Ichthyosaurus.* Orbits large. Dentition showing some differentiation, anterior teeth slender-conical, posterior teeth blunt-conical. Teeth rather widely spaced, and set mainly in distinct pits.

The genus *Mixosaurus* was based by Baur on Bassani's *Ichthyosaurus cornalianus* of the bituminous shales in the Upper Triassic of Besano in northern Italy. Though material from other regions and other horizons has been referred to this genus, it is not certain that any of these forms really represent *Mixosaurus.* In the following discussion only the typical material from Italy is referred to this genus. The other forms may be doubtfully referred to this group or may be referred to other genera, as will be indicated elsewhere.

Known only from the Triassic.

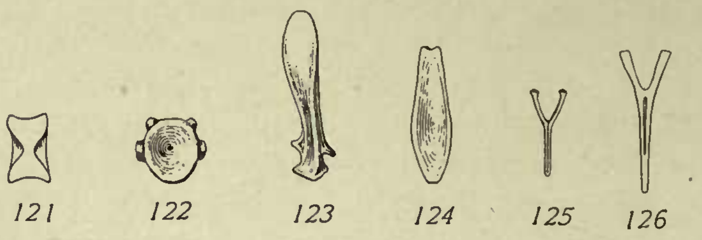
MIXOSAURUS CORNALIANUS (Bassani).

Ichthyosaurus cornalianus Bassani, Atti della Soc. Ital. di Sc. Nat., vol. 29, p. 15.
Mixosaurus cornalianus (Baur), Ber. d. 20 Versam. d. Oberrh. Geol. Ver., 1887, p. 19.
Mixosaurus cornalianus (Repossi), Atti della Soc. Ital. di Sc. Nat., vol. 41, p. 7.

The material representing this species now in the Civic Museum of Milan includes a number of very excellent specimens, well illustrating the structure of nearly all of the important parts of the skeleton. The descriptions of Bassani and Baur having given only a suggestion of the characters present in this interesting animal, Dr. E. Repossi (1902) has made a satisfactory comparison with this material possible, through the publication of a number of excellent figures accompanied by a general description of the skeleton.

The specimens known are mostly small forms only a few feet in length. There are a few remains of larger individuals, but the average size of the forms is small compared with most other known ichthyosaurian groups. In contrast with *Ichthyosaurus* of the Jurassic, *Mixosaurus* shows decidedly less of the extreme specialization in adaptation to aquatic life. Although not only a typical aquatic form, but already far advanced along this line of specialization, in nearly all respects in which comparison can be made, it is decidedly more like a shore animal than are the Jurassic ichthyosaurs. This incompleteness of adaptation is seen particularly in the organs of locomotion, but is also expressed more or less distinctly in other portions of the body. Though *Mixosaurus* is probably not more primitive than the Middle Triassic Ichthyosauria of America, it is evidently one of the most generalized members of the group.

Some characters in which *Mixosaurus* departs from the typical ichthyosaurs possibly represent specializations of this particular genus rather than persistent primitive characters. The uniformly small size, in itself a primitive character, has however tended to keep the North-Italian forms more generalized in certain respects than some of the larger forms of the American Trias.



Figs. 121 to 126. *Mixosaurus cornalianus* (Bassani). Figs. 121 to 125, after Repossi. Fig. 126, from rough sketch by the author. Figs. 121 to 125, natural size. Fig. 126, about natural size.

Figs. 121 and 122, dorsal vertebrae; fig. 123, neural arch of a dorsal vertebra; fig. 124, caudal centrum; figs. 125 and 126, lower arches of caudal vertebrae.

Vertebral Column.—Several of the best specimens taken together represent practically the whole of the spinal column, though in most specimens it is hardly possible to obtain thoroughly satisfactory information concerning all regions of the series. According to Repossi, the vertebral column consists of about one hundred to one hundred and five vertebrae. Judging from his figure (1902, tav. 8, fig. 1) of a nearly complete specimen there were between forty-five and fifty presacrals. In one of the Milan specimens the writer has counted about seventy-six vertebrae behind the posterior limb. These two estimates would seem to bring the total number up to one hundred and twenty. The number of presacrals appears approximately the same as that in *Ichthyosaurus,* though a complete specimen might show a few more than the average for the later genus. This is in strong contrast to the presacral formula of *Cymbospondylus,* which comprises more than sixty-five vertebrae.

As in all other ichthyosaurians the centra are biconcave. The concavity appears to extend well out toward the margins (fig. 121), and is not expressed mainly near the middle of the centrum,excepting possibly in the caudals.

Throughout the larger part of the column, back to the middle of the caudal region, the neural spines are relatively high and slender, but are not greatly broadened anteroposteriorly. The zygapophyses are distinctly developed (fig. 123), but are not particularly large or strong. The writer is uncertain as to whether the zygapophysial facets are separated.

In the characters of the caudal region *Mixosaurus* differs greatly from *Ichthyosaurus,* and to a considerable extent indicates less complete adaptation to aquatic conditions. In its broader outlines the tail seems to differ considerably from the caudal region of all later Ichthyosauria. In contrast to the form of caudal fin seen in *Ichthyosaurus,* in which the distal portion of the vertebral column is rather sharply deflexed, the *Mixosaurus* specimens available show near the end a gentle upward curvature of the column, which then bends down again and straightens out near the distal portion. (See fig. 45, p. 42, and fig. 50, p. 43.) The structure seen here would evidently offer support to a distal expansion of the tail, and would considerably increase its power beyond that of the form of propelling tail which is commonly found in types which inhabit both shore and water. This fin would possibly have less power than the wider expansion of the double-lobed fin of the typical *Ichthyosaurus.* Evidently the form seen here marks the transition from the straight, but somewhat broadened, tail of a shore dweller to the specialized fluke of the later ichthyosaurs.

As has been shown by Repossi (1902, tav. 9, fig. 8), the superior arches of the caudal vertebrae near the bend in the tail are extraordinarily high, and tend to take an erect position; those over the posterior portion of the bend inclining forward. This peculiar feature is noticed in those exhibition specimens in Milan in which the caudal region is well shown. Its function is evidently the broadening of the caudal fin at the point where the greatest amount of power can be applied to the best advantage. It is paralleled in several other groups of aquatic saurians in which the adaptation has been generally considered somewhat less complete than in the ichthyosaurs. In the mosasaurian genus *Clidastes* the relations of this portion of the tail region are somewhat similar. (See fig. 51, p. 44).

In addition to increase of the height of the tail through the elevation of the superior arches we find the centra of a considerable portion of the tail region very much compressed laterally and relatively high (fig. 124).

As in the American Triassic forms, the lower arches of the caudal region are united ventrally to form long-stemmed chevrons. The form of these chevrons is not unlike that in *Delphinosaurus perrini.* It is possible that Repossi's fig. 9*c*, tav. 9 (1902) represented as an upper arch is really a chevron, as it duplicates the form of chevrons shown in the specimens in the Milan museum. (See figs. 125 and 126.) It may be noted that the space available for the spinal canal is relatively much larger than in the large unquestionable neural arches figured by Repossi (1902, tav. 9, fig. 9*b*). The lower arches extend behind the bend in the tail and appear to be at least as long in that region as are the considerably shortened neural arches.

The nature of the inferior arches below the region in the tail in which the upper arches are elongated most is not clear. According to Repossi's representation of this region (1902, tav. 9, fig. 8), the facets for chevrons are much reduced or absent here. The inferior arches sketched in dotted lines in Repossi's figure do not actually exist in the specimen. On another specimen in which the caudal region is otherwise well shown, the hypocentra are again absent from this region. Though lower arches are present farther back in the tail, it is possible that they became reduced below the region of upward curvature.

Ribs.—In contrast to the bicipital articulation in the typical ichthyosaurs, the heavy ribs of the dorsal region articulate on a single head (see fig. 60*a*, p. 49), as has been shown by Repossi. In the cervical region the rib articulation seems to be single-headed as in the dorsal region. On one specimen a short rib, apparently belonging to the third or fourth vertebra behind the skull, has a single head. As interpreted and figured by Repossi, the ribs of the posterior dorsal or lumbar vertebrae are double-headed.[46] In discussing this peculiarity of *Mixosaurus*, Yakowlew (1902, 1 and 2) has suggested that as the single-headed rib precedes the double-headed in the history of the Ichthyosauria, the latter form is evidently to be derived from a single articulation by some process of division of the rib head. Since this division seemed to appear first in the pelvic region of *Mixosaurus* the suggestion was made that its appearance was connected with the extraordinary movements of this portion of the body in the use of the tail as a sculling organ. The relations of the ribs of *Mixosaurus* as described being entirely different from those of the American forms, in which a double articulation occurs in the neck only; the writer has examined, as carefully as possible, the excellent specimens on exhibition in the Milan museum, for evidence bearing on this point. This examination shows that in some cases at least the short ribs near the pelvic region or the base of the tail have broad undivided heads, as in the shastasaurian forms of the American Trias. In other instances ribs belonging to the anterior caudal region seem actually to show a beginning division of the articular face. In one case where the evidence seemed strongest, the apophysis on the vertebral centrum showed also some indication of division. It should, however, be noted that even in this instance the evidence hardly appears to warrant a definite statement that double articulation occurs, as the side of the vertebral centrum is badly broken up, and does not present a satisfactory case. The heads of these ribs are,

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[46] Through a typographical error the original descriptions did not agree with the figures.

moreover, not fully exposed, and it is not impossible that careful preparation with a needle will show that the apparent gap between the two rib heads is filled by a bridge of bone, now covered by matrix lying in a lateral groove. It is also worth noting that with the form which these ribs appear to have as they lie in the matrix, the upper head could not come into direct articulation with the diapophysis without elevating the shaft above the level of the other ribs.

Though it is difficult to make certain of the identity of all of the specimens which have been described by Repossi, it has appeared to the writer that the most strongly forked rib figured by him (1902, tav. 9, fig. 10) possibly corresponds to a cross-section of a certain neural arch which is associated with other specimens that have evidently been the originals for some of his excellent figures of vertebrae and ribs.

On the whole, the few instances in which bifurcation of the articular heads of ribs may occur, seem to the writer to be not sufficiently clear to warrant a definite statement that these ribs are normally divided, though a tendency in that direction may possibly exist. On the other hand, that such a disposition to divide should exist is rather remarkable when we consider that the American Triassic forms show an evident tendency to lose the bicipital articulation, and that they retain it only in the anterior vertebrae. In the typical *Ichthyosaurus* and in *Baptanodon,* where double-headed ribs are well developed through the greater part of the costal series, the pelvic and caudal regions are the only places where they do not normally occur.

Abdominal ribs are present in the Milan specimens of *Mixosaurus.* In Repossi's figures they resemble those of the American Triassic forms in the union of the pieces next the middle line of the abdomen to form a median spine, though the spine appears to be longer and more acute than in *Cymbospondylus.*

Extremities.—As was first shown by Baur (1887, 1), the limbs of *Mixosaurus* furnish fairly definitely evidence that the ancestral ichthyosaurian type was a shore form. In Baur's figure of the limb the characters of the propodial and epipodial segments were somewhat exaggerated, as the bones in this region are really less slender and relatively less elongated. In other portions of the limb, which were possibly not examined by Baur, other characters appear which also point definitely toward an ancestral form with a simple type of limb like that in a shore form. The characters emphasized by Baur are therefore not to be considered as incidental or accidental developments paralleling what is seen in an ambulatory type of limb, but they express in one way what is also definitely shown in other parts of the limb, or in the limb as a whole, and is distinctly visible in most other parts of the body.

Fortunately a number of the *Mixosaurus* specimens in the Milan museum are preserved in a fine shale, and as the individuals are small, the limbs have in some instances been buried almost entire before decomposition could permit a scattering of the elements. The figures of an anterior and a posterior limb shown by Repossi (1902, tav. 9, figs. 2 and 3) evidently represent almost perfect extremities. Contrary to what might have been expected from what is known of some other primitive Triassic ichthyosaurians, the posterior limbs are very considerably reduced in size below the dimensions of the anterior limbs. Evidently the hind limbs had already to some extent lost their usefulness, and were degenerating.

The *anterior limb* while considerably larger than the posterior one is also in some respects more specialized. In other words it has retained larger size as advantageous in the performance of its peculiar functions connected with locomotion by swimming. The hind limbs not being required in swimming as much as the fore limbs have gradually become reduced, but have not in the course of this reduction been forced to acquire as many new characters in adaptation to aquatic conditions. The anterior limb (fig. 127) is more primitive than that of the typical *Ichthyosaurus* in several important particulars: the epipodial elements are elongated and separated by a wide gap; the number of digits is the normal five; the phalangeal elements are less numerous than in most ichthyosaurs; in many cases the phalanges are relatively elongated and show a median constriction. The humerus of *Mixosaurus* does not show particularly primitive characters. Compared with most species of *Ichthyosaurus* it is a relatively short and broad element. The humerus figured by Repossi (1902, tav. 9, fig. 2), with the remainder of the limb, though a relatively wide bone is very much narrower than in certain other specimens in the Milan collection. In one specimen the width of the humerus equals more than two-thirds of the length. On the whole, the shortening of the humerus in *Mixosaurus* is fully as pronounced as in *Ichthyosaurus* or *Baptanodon*. In some cases it is almost as extreme as in some of the specialized ichthyosaurs of the shastasaur group. In one specimen showing what is apparently the lower side of the humerus a well developed pectoral ridge extends along about two-thirds of the length of the bone.

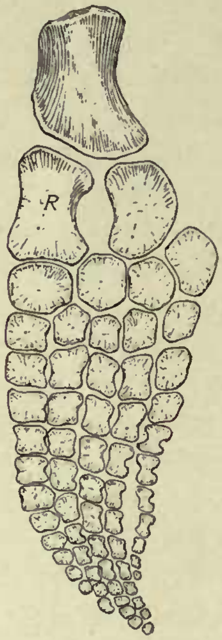

Fig. 127. *Mixosaurus cornalianus* (Bassani). Anterior limb, × ½. (Adapted from Repossi.)

In *Mixosaurus* hyperdactyly seems not to have developed, and hyperphalangy is not as far advanced as in *Ichthyosaurus*. The number of the phalanges is nevertheless far in advance of the normal, at least ten separate elements being present in the median digits. More strikingly primitive than the other characters of the digits is the tendency of particularly the proximal three to six phalanges of each digit to show an elongated form with a median constriction. In the distal phalanges, which are possibly added elements, the notches are less distinct or absent. As originally suggested by Lydekker for the notches on the margins of certain podial elements in the paddles of longipinnate ichthyosaurs, these notches or constrictions evidently indicate an original shafted form of the phalanges, which has been entirely lost in *Baptanodon* and in most of the late ichthyosaurs. The constriction of the phalangeal elements is in reality somewhat more strongly expressed on the specimens than it appears in Repossi's illustrations.

On one specimen where both fore and hind limbs are represented the *hind limb* appears to be less than two-thirds the size of the anterior one, and the bones of the pelvis appear correspondingly small. Both propodial and epipodial elements are here more slender and generally more primitive than in the anterior limb. (See fig. 97, p. 66.) The phalanges are also more slender and seem not to have increased in number to such an extent.

In the first row of the mesopodial section of the hind limb figured by Repossi (1902, tav. 9, fig. 3), as in the anterior limb, four elements appear instead of three. (See fig. 111, p. 70). The structure which appears in this case is unusual but is probably explained by another specimen (fig. 110, p. 70) in the Milan museum, in which only three elements are present in the proximal row. The lunate intermediate element in the second specimen almost closes the gap between the tibiale and fibulare, but in a second row of bones three elements articulate with the distal border of the intermedium; of these the anterior one has crowded up between the tibiale and intermedium so as almost to come in contact with the tibia. In the specimen figured by Repossi this element of the second row seems to have reached the tibia. This explanation not only accounts for the fourth element of the proximal row but may also explain the presence next the posterior border of tarsale one, and apparently functioning as tarsale two, of an element showing a strong median constriction. This constricted bone has the appearance of a metapodial or phalange, and if the explanation given above is correct it is really a metapodial moved upward into the position of tarsale two. This does not, however, explain the presence of lateral notches in other evident mesopodials shown in figure 110.

Limb Arches.—All four elements of the *pectoral arch* are figured by Repossi. (See fig. 80, p. 59.) The coracoid and scapula are represented as almost identical in form. So similar are they that unless corresponding elements from the opposite side of the body are known, and show similar evidence as to relative position, these two bones might be suspected of being either two coracoids or two scapulae. Their form is not entirely similar to that of any elements in the pectoral arches of other ichthyosaurians.

The clavicle is slender compared with the corresponding element of *Cymbospondylus.* The median end in contact with the interclavicle is considerably expanded, but the middle and lateral portions are very slender. The median stem of the interclavicle is much more expanded laterally than in the other known genera, and gives to the element as a whole a nearly triangular form. In other ichthyosaurians the median arm is narrow and the element takes on the *T* form. From beds referred to the lower Muschelkalk, Von Huene (1902, p. 11) has described a more robust and more nearly perfectly triangular interclavicle. (See fig. 81, p. 60.) The form of this element suggests its possible origin for the median plate in the stegocephalian pectoral arch.

Without more definite evidence as to their position it is not possible to make certain of the identity of the two inferior elements of the *pelvic girdle.* (See fig. 71, p. 56.) Neither element shows the obturator notch or foramen present in all of the other Triassic genera. As shown in the figure the bone labeled *Pu?* resembles the ischium of *Delphinosaurus,* but is also like the pubis of *Toretocnemus* minus the pubic foramen. The element *Is?* approaches the form of the ischium in *Toretocnemus* and *Shastasaurus,* and is also like the pubis of *Delphinosaurus* or *Shastasaurus* minus the anterior hook. Both inferior elements are much expanded, as in the other characteristic Triassic ichthyosaurian genera. The ilium is relatively short and is somewhat widened distally as in most of the Triassic forms. On the whole the pelvis shows as close a resemblance to that of *Cymbospondylus* as to that of any of the Triassic genera.

Skull.—The principal features of the cranium of *Mixosaurus* have been represented by Repossi, but as yet the individual elements have not all been described in detail. The skull is as a whole relatively large compared with the trunk. If any estimate can be made from the nearly complete specimen figured by Repossi (1902, tav. 8, fig. 1), the length of the skull equaled about 65 per cent. of the length of the trunk. In *Cymbospondylus* the length equals about 36 per cent.; in *Ichthyosaurus*[47] it may equal 80 per cent. The facial region is elongated and evidently slender, but is not developed proportionately as in the later ichthyosaurs. The superior narial openings are situated much as in *Ichthyosaurus.* The orbits are large, though possibly somewhat smaller than in *Ichthyosaurus.* The rostral region is formed largely of the premaxillaries, though the maxillaries are relatively larger than in most ichthyosaurs. Repossi's figures seem to indicate that the nasals are greatly expanded as in the other genera. A considerable number of sclerotic plates in the orbit show the existence of a large orbital ring. The elements of the posterior portion of the skull are not clearly shown.

The long and slender mandibular rami do not appear to differ materially

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[47] *I. integer.* See Fraas, E., 1891, Taf. 7.

from the jaws of *Ichthyosaurus*. In the coronoid region no distinct process is developed, but there is some indication of a flattened area on the superior margin as in *Cymbospondylus*.

Dentition.—In the characters of its dentition *Mixosaurus* seems to represent a peculiar ichthyosaurian type. As was shown in part by Baur, the dentition is characterized by the relatively small number of differentiated teeth set in the narrow alveolar margins. In an upper jaw figured by Repossi (see figs. 13 and 14, p. 28) there must have been about twenty to twenty-three teeth present. On a lower jaw there have been forty or more. In *Ichthyosaurus* Fraas places the number for long-jawed forms at about fifty teeth per jaw. In all of the specimens shown, the teeth are set in open order, particularly in the anterior portion of the jaws, where they may be separated by a space equaling from two to five or six times the diameter, of the basal portion of their crowns. Many of the roots are in distinctly separated alveoli. The anterior teeth of both jaws are long and slender. Toward the back of the jaws the crowns become lower and their basal diameter increases somewhat. The most posterior crowns may have a basal diameter twice as large as that of the anterior teeth, and a crown only half as high. Repossi's figures do not indicate the presence of a large amount of cement on the roots, nor is there indication of folding of the basal portion of the dentine as in *M.* (?) *atavus*. The enamel of the crowns seems in some cases to be sharply striated.

Classification.—As yet only one species, *M. cornalianus,* has been described which can be referred with certainty to this genus. Most of the other forms which have been referred to *Mixosaurus* might with equal right be placed in some other genus. It is not improbable that some of the Italian specimens now available will be found to vary specifically from the type of Bassani's *cornalianus*.

CYMBOSPONDYLUS Leidy.

Cymbospondylus Leidy, Proc. Philad. Acad. Nat. Sc., vol. 20, p. 177, 1868.
Cymbospondylus (Merriam), Univ. Calif. Publ. Geol., vol. 3, p. 104, 1902.
Cymbospondylus (Merriam), Univ. Calif. Publ., vol. 4, p. 33, 1905.

Presacral region of vertebral column including about 65 vertebrae. Distal end of caudal region slightly decurved. Neural arches turned forward in region of curvature. Vertebral centra of distal caudal region much compressed laterally. Caudal vertebrae with Y-shaped chevrons. Rib articulation single-headed excepting in the anterior region of the vertebral column.

Anterior arches and limbs but little larger than posterior. Interclavicle unknown. Humerus, radius, and ulna relatively long and narrow, ulna and radius both with median constriction. Digits unknown. Inferior pelvic elements broad, plate-like. Femur somewhat more primitive than humerus.

Skull with narrow rostrum consisting in a large part of premaxillaries. Facial region relatively shorter than in *Ichthyosaurus,* and maxillary relatively larger. Orbits relatively small, postorbital bar broad, but without lateral temporal opening. Basioccipital with concave condyle. Dentition isodont. Teeth numerous, set in pits in some cases at least.

Known only from the Middle Triassic of the West Humboldt and New Pass ranges of Nevada.

Three species of *Cymbospondylus, C. petrinus, C. piscosus,* and *C. grandis* were described by Leidy from fragmentary vertebrae.

C. petrinus is represented by forms attaining a length of thirty feet or more. The anterior and posterior faces of the vertebral centra are sharply concave in the central region, but are nearly flat in the peripheral half of the face. The anteroposterior diameter of the dorsal centra is less than one-half of their height.

The single fragmentary specimen of *C. piscosus* represents a form smaller than the average of *C. petrinus.* The vertebral centra are relatively longer, their anteroposterior diameter equaling more than half of the height. The anterior and posterior faces of the centra are sharply and regularly concave from the periphery to the center of the face.

C. grandis was founded on a fragment of a caudal vertebra from the West Humboldt Range, and possibly represents a large individual of *C. petrinus.*

Fragmentary material recently obtained at New Pass, Nevada, is referred to a new species, *C. nevadanus.* It is distinguished mainly by the short and massive elements of the epipodial region of the hind limb.

CYMBOSPONDYLUS PETRINUS Leidy.

Cymbospondylus petrinus Leidy, Proc. Philad. Acad. Sc., 1868, vol. 20, p. 178.
Chonespondylus grandis Leidy, Ibid.
Cymbospondylus petrinus (Merriam), Univ. Calif. Publ., vol. 3, p. 106.
Cymbospondylus? grandis (Merriam), Ibid.

This species is the best known of the American Triassic ichthyosaurs, being represented by many individuals, which collectively exhibit the greater part of the skeletal structure. It occurs in the exposures of Middle Triassic limestones in the West Humboldt Range of Nevada. Closely allied to the typical *C. petrinus* is a form, *C. nevadanus,* which has been obtained in Middle Triassic limestones exposed at New Pass, twenty-eight miles west of Austin, Nevada.

C. petrinus is represented by individuals averaging over twenty feet in length. In one very large skull, no. 9954, which does not seem to be specifically separable from this form, the dimensions of corresponding parts are about 50 per cent. larger than in specimen 9950 of *C. petrinus,* in which the length was over thirty feet. The anterior portion of the rostrum of specimen 9954 is absent, but the remaining part of the skull is over five feet in length.

Skull.—The structure of the skull in this type is fortunately almost perfectly shown in specimens 9950 and 9913 from American Cañon (pls. 2-6). Other skulls, some of which are nearly as complete, show similar structure. In no. 9950 the skull is preserved intact, and has been almost entirely freed from the matrix with relatively little difficulty. Excepting a slight depression of the frontal region practically no distortion has occurred.

Though it is relatively primitive in many respects, the skull in this form is typically ichthyosaurian. Like the typical Jurassic genera, the facial region is relatively long and slender, the premaxillaries and nasals are very largely developed, the frontals are small or are largely covered by the nasals, the superior nares occupy a nearly median position, and a heavy sclerotic ring is present. In contrast to the later forms the maxillaries are relatively larger, the snout shorter, the orbits smaller, and the lateral temporal region broader anteroposteriorly. In these respects the skull is more primitive than any described form from a later period.

Compared with the length of the trunk the skull is relatively short. As nearly as can be estimated, the length equals a little more than one-third that of the dorsal region. The skull of *Mixosaurus* seems to be relatively much longer, equaling about two-thirds the length of the trunk, while in *Ichthyosaurus* the relative length may be as great as 80 per cent.

In this species the antorbital portion of the skull is elongated as a rostrum, which narrows gradually along practically the whole distance out toward the anterior end, though the diminution in width is less noticeable immediately beyond the anterior ends of the maxillaries. The rostral region represents about 60 per cent. of the total length of the skull, but is relatively shorter than in any other ichthyosaurian with which the writer has any acquaintance, excepting *Ichthyosaurus breviceps,* from the Lower Lias, in which the length is 55 per cent. The extent of the maxillary anterior to the orbit is relatively larger than in any other ichthyosaurian. It amounts to 48 per cent. of the length of the antorbital region in this form, while in *I. breviceps* with a somewhat shorter rostrum, in which one would expect to find the maxillary relatively long, it is less than 40 per cent.

The *premaxillaries* extend more than half the total length of the skull. For a little more than half of their length behind the anterior end of the rostrum they meet dorsally. Behind this point they are separated by the nasals. In specimen 9950 the posterior ends pass above the anterior ends of the superior narial openings, but do not appear to extend any distance below them as seems to be the case in most other ichthyosaurians. In another specimen (no. 9954) the superior narial opening is cut into the posterior part of the premaxillary to some extent. In the rostral region the premaxillaries are sculptured so as to produce a peculiar roughened surface.

The *maxillaries* are longer in specimen 9950 than in any other described ichthyosaurian, both in relation to the length of the cranium and to that of the rostral region. Almost if not quite half of the dentigerous margin of the upper jaw is situated on these elements. A large *lachrymal* is clearly defined on this and other specimens. In specimen 9954 it reaches forward to the posterior border of the superior nares.

The *nasals* are large and extend back over the frontals almost to the pineal foramen.

In the frontal region of *Cymbospondylus* the nasals seem to cover as large a portion of the *frontal* element as in *Ichthyosaurus*. This might be suspected to be due in part to the displacement of the very thin posterior edges of the nasals, but the area exposed in preparation is probably nearly normal, since in several specimens prepared the border has always exhibited the same characteristically marked outline.

In contrast to the situation in *Ichthyosaurus* the large *pineal foramen* is surrounded mainly by the parietal instead of wholly or in a large part by the frontals. A prominent crest rises rapidly behind the anterior ends of the parietals reaching a very considerable elevation above the middle of the superior temporal openings. The pineal foramen is situated in the anterior portion of this crest, where it occupies such a position that it is directed partly upward and partly forward.

One of the most striking features of the skull in specimen 9950 (see pls. 2 and 6) is the relatively small size of the *orbit*, as compared with that of the later ichthyosaurs. The orbit as it appears in plate 2 is very slightly depressed, but the amount of overlap of the broken upper end of the jugal amounts at most to not more than twenty-five millimeters or a little more than one-sixth of the height of the orbit. In another specimen (no. 9913, see pl. 6) crushed laterally so that the height of the orbit would tend to be increased, the size of the orbit is also relatively small. In specimen 9950 the anteroposterior diameter of the orbit is about one-sixth the length of the skull, in spite of the fact that the rostral region is relatively short. In *Baptanodon* as figured by Gilmore[49] (see also fig. 5) the length of the orbit is only a little less than one-fourth that of the whole skull including the much elongated snout. The relative size of the orbit is particularly noticeable in comparison with the anteroposterior diameter of the lateral temporal region. The anteroposterior diameter of the lateral temporal area equals about 83 per cent. of the fore and aft diameter of the orbit in *Cymbospondylus* (no. 9950); in *Baptanodon* it appears to be less than 25 per cent.

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[49] Gilmore, C. W., Mem. Carneg. Mus., vol. 2, pl. 8.

The *jugal* is considerably expanded horizontally, and is comparatively thin vertically, its transverse diameter equaling more than twice its vertical thickness. Its vertical diameter below the middle of the orbit appears somewhat less than in *Baptanodon*, and less than in most forms of *Ichthyosaurus*. The posterior end reaches upward and backward to meet the quadratojugal above the inferior temporal notch.

The exposed portion of the *postorbital* appears to have an approximately triangular form, though its upper posterior portion may extend backward beneath the supratemporal as in *Shastasaurus*, and its anterior limits above the orbit are not clearly determined. No suture line between the *prefrontal* and *postfrontal* can be distinguished on any specimen examined, nor is there a line of demarcation observable between postfrontal and postorbital. The anterior end of the prefrontal is overlapped by the lachrymals and the nasals. The posterior end of the postfrontal extends back over the squamosal almost to the posterior end of the temporal region.

A well preserved *sclerotic ring* is shown in specimen 9913, and a complete, unbroken, and apparently undistorted ring in no. 9954. In each specimen a series of plates comprising one-half of the ring shows eight or nine plates, making a total of sixteen to eighteen. Owen counted seventeen in *Ichthyosaurus communis*, and Fraas gives the number as varying from fifteen to twenty in *Ichthyosaurus*. Gilmore finds but fourteen plates in *Baptanodon*, and Andrews gives the same number for *Opthalmosaurus*. In specimen 9913 the inner or median portion of each sclerotic plate bends sharply around the equator of the eyeball and extends over the inner side of the eye showing a flattening of the eyeball similar to that described for *Ichthyosaurus* by Owen[50] and for *Baptanodon* by Gilmore.[51] The sclerotic ring is smaller compared with the size of the skull than in any of the later ichthyosaurs. In specimen 9913 the greatest diameter of the slightly distorted ring is a little more than 10 per cent. of the total length of the skull. In no. 9954 the greatest diameter is less than 10 per cent. of the total length. In *Ichthyosaurus platyodon* and *I. breviceps* the ring is relatively 40 or 50 per cent. longer.

The lateral temporal bar of *Cymbospondylus petrinus* is always characterized by uncommon length anteroposteriorly. Its height is somewhat less than in most ichthyosaurs. Relative to the length of the cranial region it is much less elevated than in *Baptanodon*. Behind the jugal the inferior side of the temporal bar is sharply cut out so as to form with the slightly concave coronoid region of the mandible an elliptical opening with its long diameter extended anteroposteriorly. According to the suggestion of McGregor[52] the

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[50] Owen, R., Liassic Reptilia, part 3, p. 103. London, 1881.

[51] Gilmore, C. W., Am. J. Sc., vol. 23, p. 194, 1907.

[52] McGregor, J. H., Mem. Am. Mus., vol. 9, p. 91.

temporal bar originally enclosed a lateral temporal opening, which was closed through gradual anteroposterior compression of the bar, owing to the enlargement of the orbit. In this form the bar shows fully as much area on the side of the skull as in many reptilian forms possessing a lateral temporal fenestra. Though the temporal bar has probably been somewhat reduced by enlargement of the orbit, it seems very doubtful whether it ever really enclosed a lower temporal fenestra.

The *squamosal* bone is a triradiate element, as in other ichthyosaurs, one branch extending forward and outward along the outer border of the superior temporal opening, one forward and inward along the outer side of the posterior arm of the parietal, and one reaching down to meet the pterygoid on the anterior plate of the quadrate. In a lateral view of the skull the squamosal represents only a small part of the exposed area of the temporal bar, as the lateral anterior arms are largely covered by long posterior processes of the postfrontal, which reach almost to the upper posterior angles of the skull. The large *supratemporal* is apparently triangular, the acute anterior angle extending forward between the postorbital and postfrontal. The superior margin in contact with the squamosal and postfrontal forms a nearly straight line. The inferior border is in broad contact with the quadratojugal as in *Ichthyosaurus*. In *Baptanodon* this contact is very narrow, and the temporal bar is exceedingly narrow at this point. The *quadratojugal* extends downward almost to the articular surface of the quadrate and is covered above by the supratemporal. Inferiorly it reaches forward over the inferior temporal notch to meet the jugal. The lower side is considerably thickened a short distance above the border.

The occipital region of this species (pl. 5, fig. 1) is less satisfactorily known than the other parts of the skull, as the difficulties of preparation have been relatively great. In specimen 9950 most of the elements of the occipital region seem to be in nearly their original position, but the exact form of some of the bones cannot be definitely determined. In specimen 9913 the skull has been broken through obliquely in the occipital region, and the structure of some of the elements is more clearly shown.

The *basioccipital* has a peculiar and characteristic form in that its articular face for contact with the atlas is deeply concave instead of convex as in *Ichthyosaurus*. In articulation the broad concave face of the basioccipital received the strongly convex anterior face of the atlas. In specimen 9950 the deep concavity on the posterior face of the basioccipital extends out to the lateral margins. Inferiorly the posterior end of the basioccipital is rounded, and is truncate downward and forward as if for the accommodation of a hypocentrum. On specimen 9913 the concave face extends almost to the lateral margins, and the inferior side of the concavity is bounded by a prominent lunate ridge, which tends to have somewhat the form of the spout-like odontoid process of the Ungulata. Below the prominent inferior ridge the inferior side is not truncated as in specimen 9950, but a sharply concave area extends around the lower side of the bone between the lunate ridge and the outer margin of the posterior side. The form of the posterior face of the basioccipital in specimen 9913 suggests that the concave face has been secondarily developed on a strongly convex face.

On the inferior side of the basioccipital there are situated two prominent apophyses similar to those on the inferior face of the basioccipital of *Sphenodon.*

The small and somewhat distorted *lateral occipitals* are seen in place in specimen 9950. They appear to be perforated or notched for the passage of nerves or blood vessels, as in many other ichthyosaurians. In specimen 9913 an element possibly representing a lateral occipital rests upon the anterior side of the basioccipital. It has been split longitudinally and shows the passage of a large foramen. The complete outlines of the *supraoccipital* are not shown, but its upper portion is seen to extend forward a considerable distance to form part of the floor of a deep fossa between the posterior arms of the parietals.

The *opisthotic* and *stapes* are not certainly recognized on any of the several specimens that have been carefully examined, but there seems to be some reason for considering that the stapes at least was a less conspicuous element than in the later ichthyosaurs. The opisthotic may be represented by a somewhat indefinite element seen in specimen 9950. In the same specimen a slender rod of bone (*x*, pl. 5, fig. 1) extending from the otic region to the quadrate may represent the stapes. A careful examination of the well preserved quadrate has not shown the presence of a distinct pit for the accommodation of the distal end of a large stapes such as is present in some of the later ichthyosaurs.

The heavy *quadrate* of *Cymbospondylus petrinus* is closely and broadly united with the pterygoid, the squamosal, and the quadratojugal, so that the posterior angle of the skull must have been particularly rigid. The contact with the pterygoid extends inferiorly to the articular head of the quadrate and reaches up to the middle height of the quadrate, where the pterygoid meets the squamosal. The median side of the quadrate which is in contact with the pterygoid extends forward as a broad plate much as in *Sphenodon.* On the outer side, the large quadrate foramen is overlapped externally in part by the supratemporal. The broad articular head of the quadrate is crossed transversely by a marked groove situated between an anterior and a posterior convex surface.

The general disposition of the typical palatine elements on the inferior side of the skull (pl. 4) is not materially different from that in *Ichthyosaurus.* In all cases the palate is largely roofed over, the median margins of the pterygoids approaching each other quite closely back to a point about opposite the middle of the orbits. The relation of the pterygoids to the palatines is similar to that in *Ichthyosaurus*. The posterior ends of the pterygoids are extended backward as prominent projections reaching a considerable distance behind the basioccipital. Between these processes and the wings of the pterygoids in contact with the quadrates there is a strongly marked groove on each side.

On both sides of the palate of specimen 9950 the posterior portion of what might be considered as the outer wing of the pterygoid is separated from the main body of the pterygoid by a distinct break having the same position in the two cases. If the separation indicated here is a natural parting of the bone, the posterior element evidently corresponds to the ectopterygoid.

The relations of the prevomers have not been clearly determined, but appear to be similar to those found in *Ichthyosaurus*. The hyoid elements are long, slender, slightly curved rods similar to the hyoids of *Ichthyosaurus* and *Baptanodon*.

In specimen 9913 an elongated element situated above the pterygoid may represent the epipterygoid.

The *lower jaw* is slender and elongated much as in the typical ichthyosaurs. The rami are united in the symphysis for about one-fourth the length of the jaw, and the anterior ends of the splenials are included in the symphysis. The much elongated dentary extends backward to a point almost even with the posterior border of the orbit. The narrowed anterior ends of the angular and surangular extend forward almost as far as the anterior end of the maxillary. In specimen 9950 the outer side of the splenial is exposed for a short distance below the middle of the dentigerous portion of the jaw.

On the outer side of the posterior portion of the mandible the angular and surangular occupy about the same relative areas as in *Ichthyosaurus*. No coronoid elevation is present, but the coronoid region of the surangular is broadened and flattened above offering a considerable area for muscle attachment. In specimen 9950 there is on the inner side of the posterior end of the jaw either a coronoid reaching far back, or an element which has been known as the prearticular. In this form the splenial extends back to a point below the coronoid region, where it overlaps the inner plate of the angular. The splenial and the inner plate of the angular both overlap an element (see *Cn.*, fig. 9, p. 27) which extends from the coronoid region almost to the posterior end of the jaw. It extends over the median side of the articular, and is distinctly separated from that bone. The relations of a similar element the writer has seen most clearly in an ichthyosaurian, no. $\frac{R}{2180}$, in the British Museum of Natural History. In this specimen the splenial extends back almost to the cotylus of the mandible, and partly covers the inner, upward-curving portion of the angular. Lying between the splenial and the surangular there is in the coronoid region a plate-like element occupying the position of the coronoid. This element extends backward from its normal position, passing between the inner plate of the angular and the inner side of the articular, and falling but a little short of reaching the extreme posterior end of the jaw. In a specimen of *Baptanodon* (no. 878) at the Carnegie Museum in Pittsburg the same relations of these elements have been noted, and the coronoid extends quite to the posterior end of the jaw.[53]

The articular of *Cymbospondylus petrinus* rises abruptly behind the cotylus where the thickened anterior end forms a heavy posterior buttress against which the quadrate articulates posteriorly. It extends backward to the posterior end of the jaw, where it is again considerably thickened. On all of the specimens that have been examined, the posterior portion is deeply excavated superiorly between the anterior and posterior thickened regions.

Dentition.—In general, the characters of the dentition of *Cymbospondylus* excepting the insertion are essentially similar to those of *Ichthyosaurus.* Both upper and lower jaws are set with conical teeth numbering from thirty to thirty-five for each ramus of the jaw. In some cases at least (figs. 10 to 12), the teeth are situated in completely enclosed bone pits. Though the anterior teeth seem to have somewhat more slender crowns than the most posterior ones there appears to be no close approach to the degree of differentiation seen in *Mixosaurus.* The amount of cement on the roots of the teeth seems to be small. The dentine is strongly folded toward the base. The enamel of the crown is finely but sharply striated.

MEASUREMENTS OF SKULL OF *C. petrinus,* NO 9950.

Greatest length of skull on horizontal plane	1166 mm.
Length, anterior end of premaxillary to posterior border of pineal foramen	814
Length, anterior end of premaxillary to anterior border of left orbit	717
Length, anterior end of premaxillary to anterior end of maxillary	373
Greatest height of skull	365
Premaxillary, anteroposterior diameter	650
Anterior end of nasals to anterior border of pineal foramen	380
Supratemporal fenestra, anteroposterior diameter	190
Lateral temporal bar, anteroposterior diameter	160
Orbit, anteroposterior diameter	198
Orbit, height	115
Length of right ramus of mandible	1180
Mandible, height below middle of orbit	114

Vertebral Column.—The most nearly complete specimen which has been examined (no. 9950) shows a practically complete vertebral series back to the

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[53] Gilmore, C. W., Mem. Carneg. Mus., vol. 2, pp. 97 and 98, and pl. 11, fig. 2.

middle caudal region (fig. 128). Excepting the dislocation of some of the anterior vertebrae, and a small gap above the pelvis, the series is unbroken. Out of the total number of 84 vertebrae present, 67 are evidently presacrals. The location of the sacral region is pretty definitely fixed, both by the position of the pelvis and by the reduction in length of the ribs. The elements of the pelvis are still in their natural positions with reference to each other, and the ilium on one side appears to have almost its normal relation to the vertebral column. Considering that these elements, as also the vertebral centra and arches, and the ribs, show little evidence of disturbance, it is fair to assume that the vertebra above the ilium was either next the point of attachment of the pubis or close to it. The ribs in this region are still of considerable length, and if the point of attachment is not located at this place it is probably somewhat farther back.

The number of presacral vertebrae present here exceeds considerably that of any other ichthyosaurian of which the writer has any information. In the typical *Ichthyosaurus* the number is ordinarily near 45. The extraordinarily large number of 54 presacrals is indicated recently by Broili[54] in *I. platydactylus*. In *Mixosaurus* the number seems to have been between 45 and 50. The number in *C. petrinus* is also larger than that in any other marine saurians excepting very long-necked forms, and suggests the possibility that the number of presacrals may have been reduced rather than increased in the later Ichthyosauria. A general reduction of the number in later forms might be correlated with the development of a highly specialized caudal fin, causing localization of the locomotor function in the distal caudal region, instead of distributing it through nearly the whole length of the tail.

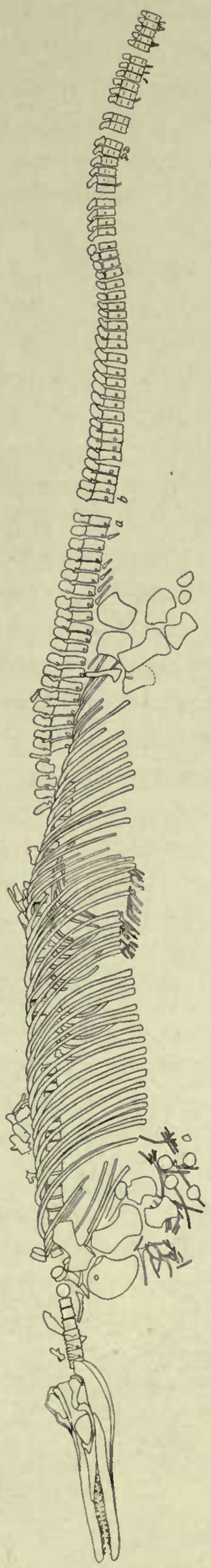

Fig. 128. *Cymbospondylus petrinus* Leidy. Outline of skeleton from specimen 9950, with caudal region and posterior limb added from specimen, 9947, × 1/41 *a*, last caudal vertebra represented from the series of no. 9950; *b*, first vertebra represented from the series of no. 9947. The first vertebra represented in the series of no. 9947 seems to correspond in form and position of the diapophyses to a point somewhat farther back in the series than that represented by vertebra *a* of no. 9950.

In specimen 9950 there are eleven vertebrae in front of the anterior border of the coracoid and scapula. Although no definite determination of the

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[54] Broili, F., Palaeontog., Bd. 54, Taf. 13.

posterior limit of the cervical region can be made, eleven vertebrae is a relatively large number for this portion of the column.

The atlas and axis are clearly shown in position in several specimens. (See pl. 8, also text-figure 58.) The centrum of the atlas is as wide, and in some cases almost as high, as that of the axis. Its anteroposterior diameter is considerably less than that of the axis. The anterior face is strongly convex, the convexity reducing the lateral and inferior borders to one-half or one-third the anteroposterior diameter of the centrum. The anterior face shows no depression into which the basioccipital might be received. The anterior face of the atlas is received in a deeply excavated articular face on the basioccipital. The posterior face of the atlantar centrum and the anterior face of the axis are both concave, and there is no suggestion of fusion of the two centra such as occurs in the later ichthyosaurs. The elements of the upper arch of the atlas as far as known are not materially different from those on the atlas of *Ichthyosaurus.*

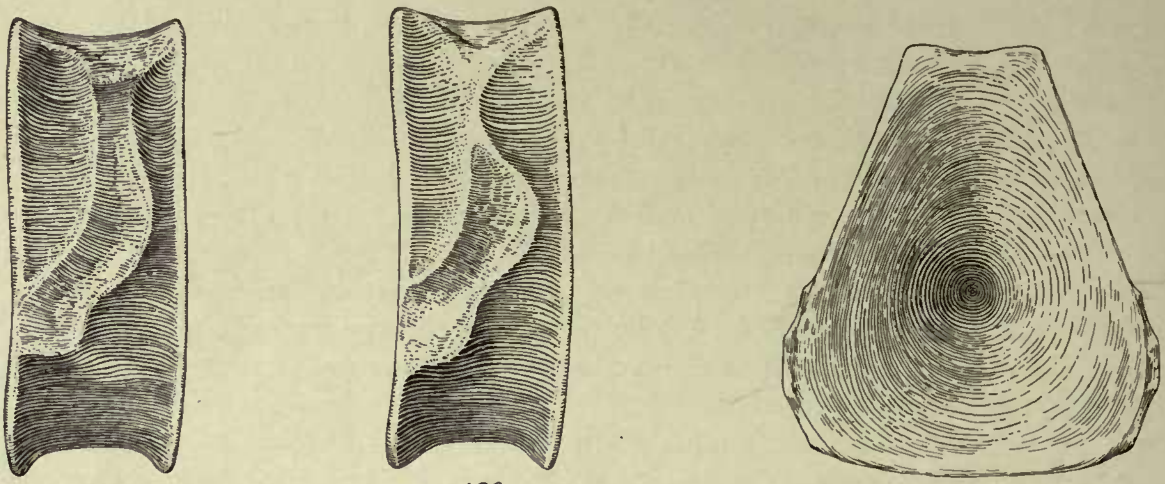
The adjacent inferior borders of the atlas and axis may be obliquely truncated toward the plane of contact, for the intercalation of an intercentrum. There seems also to have been a small intercentrum between the third centrum and the axis, but none was present behind the third.

On the axis of no. 9950 there is a short diapophysis but no distinct parapophysis. In no. 9943 (fig. 58, p. 48) both diapophysis and parapophysis are present. On centra three and four of no. 9154 parapophyses of considerable size are present and small, nearly round articular facets are developed for the lower rib heads. On centrum six the parapophysis is very rudimentary, and on what appears to be the seventh it is absent. In no. 9950 the diapophysis on the fourth centrum is 43 mm. high, the parapophysis 17 mm. On the eighth centrum the corresponding dimensions are 45 mm. and 8 mm., and the parapophysis is generally much reduced. On the eleventh centrum there may be a minute rudiment of a parapophysis on the anterior margin. In specimen 9943 relatively large parapophyses are present back to the twelfth centrum (fig. 58, p. 48). On the thirteenth there is a trace of a parapophysis on one side only. In this specimen the parapophyses increase somewhat in size toward the dorsal region, and are larger both absolutely and relatively on the twelfth compared with the size of the diapophyses than they are on the fifth and sixth centra. The form and dimensions of the diapophyses remain about the same, back to the twelfth centrum. On the thirteenth they increase markedly in height, but the increase is not sufficient to make the height of the diapophysis on the thirteenth centrum equal the complete height of the diapophysis and parapophysis on the centra immediately preceding. The anterior cervical rib heads are divided proximally by a deep notch forming two distinct heads.

In those cervicals in which the ends of the centra are visible the degree of concavity is less than in the typical *Ichthyosaurus.* The excavation is comparatively slight until about half the distance to the center is reached where it runs in quite sharply.

The vertical transverse cross-section of the cervical centra is much as in other ichthyosaurians, the transverse diameter being relatively large. In specimen 9943 the inferior side of the cervicals is distinctly carinate back to about the tenth vertebra.

In the dorsal region of specimen 9154, as also in 9950 (pl. 8), and others, the diapophyses are seen to elongate gradually as the centra come to be farther removed from the skull. In the middle dorsal region the lower portion of the diapophysis bends forward rather sharply from the nearly vertical upper portion. In the typical vertebrae of *Cymbospondylus petrinus,* the diapophyses differ from the ordinary form seen in *Shastasaurus* in that the antero-inferior border always seems to reach the anterior border of the centrum and be cut off by it (figs. 129 and 130); indicating that the lower portion of the rib head has come very near to intervertebral articulation, though there is no facet developed on the posterior border of the centrum in front.



Figs. 129-131. *Cymbospondylus petrinus* Leidy. Vertebrae from the middle and posterior dorsal regions, × ½.

Fig. 129, middle dorsal vertebra; fig. 130, posterior dorsal vertebra; fig. 131, posterior dorsal vertebra.

At about the 36th to 38th centrum in no. 9950 the diapophyses move down the side of the centrum, and the articular faces are no longer confluent with the facets for the neural arches. The form of the centrum also changes from nearly circular in the anterior dorsal region to a high, narrow, triangular form in the posterior dorsal and anterior caudal region (pl. 9, and text-fig. 131). In this portion of the column the biconcavity of the centra is reduced to a very small area in the middle of each articular face, outside of which the surface is nearly plane.

In the middle caudal region the diapophyses are short and round, and have risen almost to the middle of the sides of the centra. The vertical transverse cross-section of the centra has also changed to a narrow hexagonal form.

The upper arches of the cervicals possess strong zygapophyses (pl. 8), on which the lateral faces are well separated and do not fall into the same plane, as occurs in *Ichthyosaurus*. In the dorsal region the zygapophyses are still well developed and the facets separate. In the caudal region the zygapophysial facets are much reduced, although the anterior and posterior projections of the upper arches are retained on most of the vertebrae.

The neural spines of the cervicals are somewhat compressed laterally, but are generally thicker than in *Ichthyosaurus*. In the dorsal region the spines are still considerably thickened. In no case, however, does the thickening of the spines approach that of *Shastasaurus altispinus*. In the caudal region of specimen 9950 the neural arches are considerably lower and thinner than in the dorsal region.

The form, and most of the important characters, of the caudal region are well shown in a large specimen of *C. petrinus* (no. 9947), in which there is present an excellent series of 59 vertebrae, aggregating twelve and one-half feet in length (fig. 132). The series begins near the pelvic region and extends

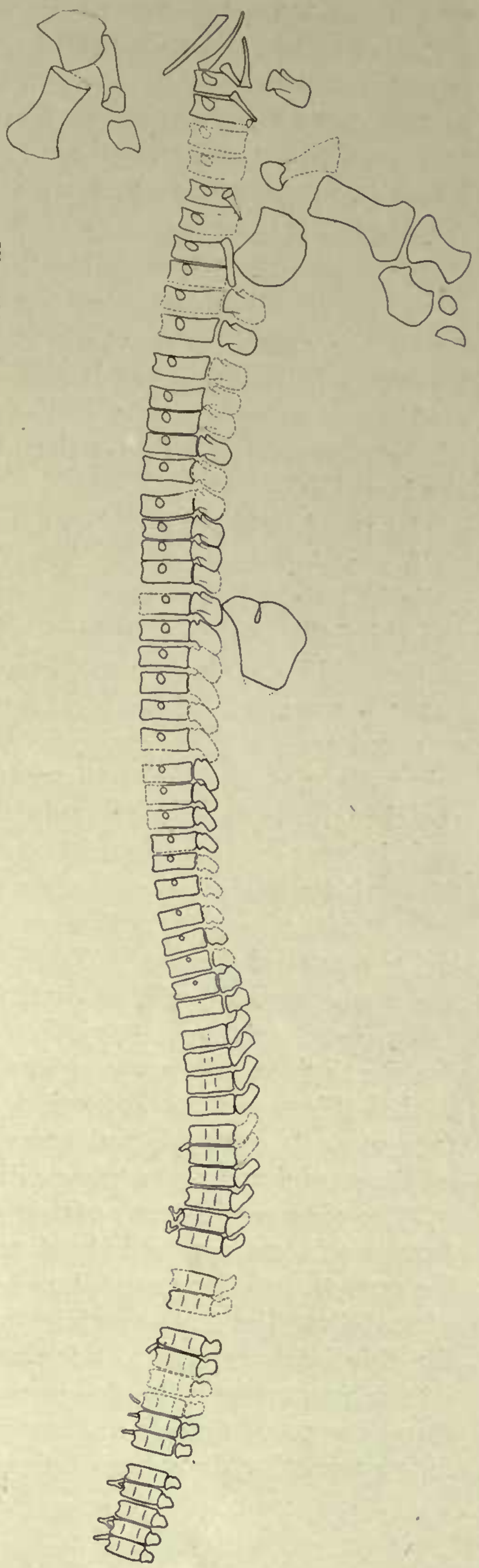


Fig. 132. *Cymbospondylus petrinus* Leidy. Caudal series with elements of the posterior arches and limbs, × 1/15.

back to within a few feet of the end of the tail. Immediately in front of this series of centra are broad-headed ribs with a length of 300 mm. or more, while the ribs with the centra opposite the pelvis are suddenly shortened to 120 mm. in length, and the rib heads are narrowed to a broad elliptical cross-section. The vertebrae immediately behind the pelvis of this specimen correspond in form, and particularly in form and size of the diapophyses and in their position on the side of the centrum, to a point in the column not farther forward than the seventy-first vertebra behind the head, or the sixth behind the pelvis, of the practically continuous series of specimen 9950. (See fig. 128).

In the vertebrae immediately behind the pelvis the width of the centra transversely is somewhat less than the height, and the diapophyses are situated about one-third of the distance up the sides of the centra. The height of the neural arches is less than that of the centra, and the thin, broad spines are bent backward.

In passing backward through the caudal region from the pelvis to the thirtieth vertebra back of the femur, as here situated, the centra decrease very little in height but become much narrower transversely, and in the region of the thirtieth vertebra become relatively short inferiorly; the diapophyses rise to the middle of the centra, become reduced to small round knobs and disappear; the neural spines become shorter, are slightly wider distally, and begin to stand erect. The change from the recurved to erect position of the arches takes place at the thirtieth vertebra. The upper arch of the twenty-eighth vertebra turns backward as do those of all anterior to it, on the thirtieth the arch is erect and on the thirty-first it bends forward. Behind this point to the fifty-third vertebra the short upper arches all turn forward. The arches of the fifty-third and fifty-fourth, the last ones present in this specimen, are erect but not curved forward. In the region immediately behind the point where the upper arches begin to turn forward, the centra are slightly wedge-shaped, being shorter anteroposteriorly at the lower side. Though the diapophyses of the thirtieth vertebra are rather prominent no lateral apophyses are present behind this point. A short distance back of the bend the middle of the lateral face of each centrum bears two parallel anteroposterior ridges about twenty millimeters apart and separated by a shallow depression.

The changes in form of the caudal vertebrae which have been mentioned seem, as far as can be judged, to be connected with fairly definite changes in the curvature of the caudal region as shown in this specimen. As the series of vertebrae lies in the matrix the tail is bent slightly upward as far back as the thirtieth vertebra but from that point backward it is curved downward. At the point where the downward curvature begins the upper arches suddenly stand erect and then turn sharply forward, the diapophyses disappear, and the anteroposterior diameter of the inferior side of the centra becomes relatively short. The upward curvature of the tail as it lies in this specimen may be unnatural, and due simply to movement of the body after death. The downward curve of the distal region, being initiated as it is with noticeable modification in the form of the vertebrae, is evidently natural. Possibly the upward curve anterior to this is also natural, the distinct change in the vertebrae occurring at the crest of a long, upward curve as in *Mixosaurus;* or the distal region may have bent down from a nearly horizontal anterior region.

Facets for lower arches are present on the caudal centra in no. 9947, and the inferior side of the centrum is in all cases sharply angular, but chevrons have been seen only in the region back of the downward bend of the tail, where they are very small, though the facets for their reception seem to be larger than in the anterior portion of the tail.

The nature of the curvature in the caudal region of this specimen is in some respects not unlike that of *Ichthyosaurus,* as the upper arches are in relation to the centra but little larger than in that genus. The centra themselves are, however, much larger in the region of the bend, and beyond, than in any of the later ichthyosaurs, and the high thin centra doubtless served to broaden the fin somewhat as the high arches have done in *Mixosaurus.* The fact that the centra were higher suggests that less curvature of the distal caudal region was needed in order to widen the fin than was required in *Ichthyosaurus,* and that the bend was a gentle upward curve followed by a somewhat sharper downward flexure, as in *Mixosaurus.*

Following are the measurements of the series of caudal vertebrae in specimen 9947.

Approximate position of vertebrae, measured back from femur as situated in the matrix.	Presence of diapophyses.	Height of centrum.	Anteroposterior diameter of centrum.	Transverse diameter of centrum.	Height and curvature of neural spine.	Length of chevron.
1	present	137mm.	51	112*a*		
12	present	128	49	115*a*	back slightly, 86	
27	present	114	48	80	back slightly, 61	
30	present	110	50 superior 44 inferior		erect, 57	
37	absent	114	48 superior 45 inferior	74.5	forward, 50	40*a*
41	absent	119	46	68	forward, 55	43*a*
48	absent	106	44	57*a*	forward, 43	40
53	absent	98	43	50*a*	vertical, 39	35

a, approximate.

Ribs.—Excepting on the anterior six to twelve vertebrae, the ribs of *C. petrinus* are all single headed (pl. 10). The short double-headed ribs have clearly notched heads, and articulate on distinctly separated diapophyses and parapophyses. As in *Shastasaurus,* in passing back through the vertebral series, the lateral apophyses of the vertebral centra remain widely separated to the point of disappearance of the parapophysis. If, as has been suggested by Yakowlew, the bicipital articulation was being developed in these forms through division of the rib head and of the vertebral apophysis with which it was in articulation, one would expect in passing forward to the region where separate apophyses actually exist to find the parapophyses gradually separating from the diapophyses. The fact that this is not the case may justly be urged against the view that the primitive ichthyosaurian possessed single-headed ribs. If a double articulation has been introduced in the American forms it must have appeared through the development of a parapophysis situated a considerable distance away from the diapophysis. If the double articulation extended from the cervical region out to the dorsals, the progress was most probably through the formation along the line of advance of rudimentary apophyses with no function of articulation. As yet no reason has been given why independent processes should grow out from the region of the paropophysis and the lower head to meet and form an inferior articulation. In addition to the arguments that have been presented, it is to be remembered that some of the oldest known ichthyosaurian forms, *viz.,* members of the *M.*(?) *atavus* group, have distinct double articulations in the posterior dorsal region.

The ribs of the dorsal region of *Cymbospondylus petrinus* are rather heavy, but have in general the form seen in *Ichthyosaurus.* The heads are thick inferiorly, and the superior portion of the articular face curves away from the upper part of the diapophysis, evidently leaving a gap filled by cartilage as in *Shastasaurus.* The posterior dorsal ribs have remarkably wide heads, but nowhere has there been observed a tendency for the articulating surface to divide into two faces, as has been suggested in the case of *Mixosaurus.*

In specimen 9950 short caudal ribs are present with the anterior caudal vertebrae. As shown in plate 10, figure 7, they have nearly round articular heads, but are considerably broadened distally.

Abdominal ribs are found in considerable numbers with most of the larger specimens, but are usually too much scattered about to show definitely their relations to each other. With specimen 9154 there is preserved a considerable section of the abdominal plastron in which the elements have suffered no disturbance (pl. 10, fig. 8). As nearly as can be determined there are usually two transverse series of abdominal ribs for every pair of true ribs. Each transverse series consists of a V-shaped median piece and two lateral pieces. The median elements are heavy, and are only slightly flattened anteroposteriorly. They are not divided along the median line, as in some ichthyosaurs. The anterior end or the point of the V of each median piece extends forward on the median line as an overlapping knob-like process. Between the lateral ends of the median pieces are inserted the ends of the heavy discrete lateral pieces.

The plastron presents as a whole an appearance of somewhat greater strength and robustness than that of the later ichthyosaurs.

Pectoral Arch.—The entire pectoral arch is well known excepting the interclavicle, which has never been recognized (pl. 11).

The *scapula* is not like that of any other ichthyosaur. The body of this element is strongly recurved so that the much expanded distal end is turned almost at a right angle to the proximal portion. The anterior part is also much broadened just in front of the proximal end. The form of this element is quite unlike that in any other Triassic genus. It approaches most closely the general form in *Ichthyosaurus,* particularly in the character of the anterior expansion, which occupies the position of the anterior hook in *Shastasaurus.* It differs from the type seen in *Ichthyosaurus* in its much greater proximal and distal expansion.

The form of the sickle-shaped *coracoid* does not correspond to that in any other ichthyosaurian genus. The nearest approach is found in *Delphinosaurus* of the Californian Upper Trias. In *Delphinosaurus* the position seems to be reversed anteroposteriorly, and the large perforation just anterior to the proximal articulation is absent. Perforations and emarginations in this region of the coracoid are ordinarily not remarkably persistent features. This character has however been recognized in all specimens of *C. petrinus* thus far examined, and together with other differences would seem to distinguish this form sufficiently.

Fig. 133. *Cymbospondylus petrinus* Leidy. Coracoid showing anterior perforation, × 1/6.

The *clavicle* is uncommonly large and heavy. The middle portion is considerably expanded, but the ends are narrow. The median end seems to show a face of articulation for an interclavicle, but that element is unknown.

Pectoral Limb.—As yet we know certainly only the first three segments of the pectoral limb in *C. petrinus,* no specimen having been found in which the phalanges are in place or even certainly recognizable. Owing to early decomposition of the thinner portions of the paddles they have probably been scattered before the slow accumulation of calcareous mud could cover them. In all of the *Cymbospondylus* specimens that have been examined the limb elements are almost exactly similar to the limb of specimen 9154 previously described (Merriam, 1905, 2).

The humerus is in all cases a relatively slender element; though not greatly elongated, it is not greatly expanded distally. The radius is extraordinarily long and slender for an ichthyosaurian, and the median constriction is pronounced. Between the epipodial elements is a gap as wide as that in the limb of any typical shore reptile. The ulna is also relatively long and shows a median constriction. The posterior portion of this element begins, however, to show the expansion so frequently occurring in aquatic types, and the posterior notch has been almost closed.

In specimen 9950 (pl. 11), as in several others, a transverse row of three small discoidal elements is seen next the distal end of the epipodial segment. These bones are almost circular in form, and they do not occupy the entire transverse space opposite the epipodials, so that they were evidently implanted in a heavy cartilaginous plate. In specimen 9148 a similar row of bones is seen. From their occurrence in this position there can be little doubt that these elements are carpals.

Pelvic Arch.—The elements of the pelvic arch (pl. 12, figs. 1-4) have been found in nearly their natural position in several specimens. The broad plate-like ventral elements were evidently united along the median line somewhat as in *Toretocnemus* (fig. 69, p. 55).

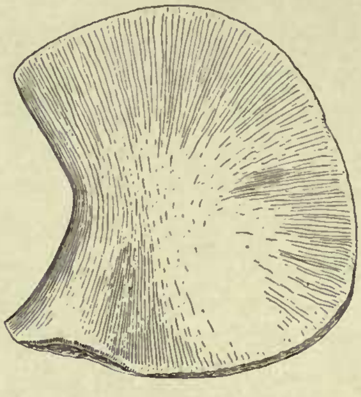


Fig. 134. *Cymbospondylus petrinus* Leidy. Ischium, specimen 9950, × ¼.

The *ischium* has much the same form as in *Delphinosaurus perrini* but may in some cases (pl. 12) show a shallow antero-internal notch giving it a form approaching that of the pubis of *Delphinosaurus.* Excepting the notch just mentioned the form is also not unlike that of the ischium in *Mixosaurus.*

The *pubis* resembles this element in *Toretocnemus* in that the proximal end is perforated by a large obturator foramen. In the only specimens which are perfectly preserved this opening is completely closed by bone. The transition from this form to that seen in *Shastasaurus* would be made easily by breaking down the bar of bone between the obturator foramen and the margin.

The *ilium* has a considerably expanded proximal head with an elongated and transversely expanded superior blade. The form resembles that of *Delphinosaurus,* though distinguished from it by the wider expansion of the blade and the absence of a posterior tubercle. Judging from its position in specimen 9950, the superior blade of the ilium was directed upward and forward to its sacral attachment.

Pelvic Limb.—The posterior limb is represented by the femur in the most nearly complete specimen, no. 9950. In specimen 9947 (pl. 12) a pelvic limb is present in which the femur has the same form and almost the same dimensions as in no. 9950.

The hind limb of no. 9947 shows the propodial and epipodial elements in their natural positions in the matrix, and with them are two small elements from the distal half of the paddle.

The *femur* is more slender than that of *Delphinosaurus*, *Toretocnemus*, or *Shastasaurus*. The nearest approximation to this type is found in *Mixosaurus*, but even here the distal expansion is relatively greater.

On the upper side of the femur the plane of the flattened distal end is continued over the proximal end with but little elevation. On the lower side of the proximal end a heavy trochanteric ridge is developed.

The distal end of the femur shows a broad terminal facet extending across nearly its whole width, and situated normal to the long axis of the bone. On this large facet the tibia articulates, standing in such a position that its long axis falls into a line almost coinciding with the long axis of the femur. Behind the broad terminal face of the femur there is a smaller facet standing almost normal to the plane of the terminal facet.

The *tibia* is longer than its greatest transverse diameter, and its proximal diameter is considerably greater than the distal. The median region is strongly constricted. The anterior side of the distal end is not expanded laterally beyond the limits of the median or shaft portion of the bone, but ends abruptly in a flat, roughened or pitted facet. Whether a small element has articulated on this face is as yet not certainly known.

The *fibula* articulates on the small posterior face of the femur, the situation of the bone being such that it is articulating largely against the posterior side of the femur with its narrower end. The median portion of the fibula is constricted. The distal end of the bone is greatly broadened compared with the transverse extent of the proximal and median portions, and shows a strongly curved terminal margin.

Of the other two elements present with the limb in specimen 9947, one is a small discoidal bone situated between the distal ends of the tibia and fibula, and presumably representing a mesopodial. The other bone is larger and is situated near the distal end of the fibula, but its form is too indefinite for determination.

The size and relative length of the epipodial elements of the posterior limb of specimen 9947 are much the same as in the elements of the corresponding region of the anterior limb of specimen 9950. Both epipodials show, however, a somewhat stronger median constriction than is seen in the anterior epipodials.

The most peculiar feature of the posterior limb is the situation of the tibia almost opposite the middle of the distal end of the femur, with the fibula located far back, and practically articulating on the posterior side of the femur.

Compared with the posterior limb of *Mixosaurus,* the available specimens representing the limb of *Cymbospondylus* may be considered, so far as known, to represent nearly the same stage of evolution as the hind limb of *Mixosaurus.*

MEASUREMENTS OF LIMB AND ARCH ELEMENTS, SPECIMEN 9950.

Humerus.	
Greatest length	325 mm.
Greatest transverse diameter of distal end	200
Least transverse diameter of median region of shaft	133
Radius.	
Greatest length	200
Greatest transverse diameter of proximal end	143
Greatest transverse diameter of distal end	160
Least transverse diameter of median region of shaft	83
Ulna.	
Greatest length	185
Greatest transverse diameter of proximal end	121
Least transverse diameter of median region of shaft	95
Coracoid.	
Greatest anteroposterior diameter	312
Greatest transverse diameter	246
Scapula.	
Greatest anteroposterior diameter	357
Greatest width of distal end of posterior blade	195
Ilium.	
Greatest length	205
Ischium.	
Greatest anteroposterior diameter	200
Greatest transverse diameter	175
Pubis.	
Greatest transverse diameter, approximately	126

MEASUREMENTS OF POSTERIOR ARCH AND LIMB ELEMENTS OF SPECIMEN 9947.

Femur.	
Greatest length	255 mm.
Transverse diameter of proximal end, parallel with flattened distal surface	117
Transverse diameter of distal end, parallel with flattened surface	170
Transverse diameter at narrowest portion of median region, parallel with flattened distal surface	83
Transverse diameter of tibial facet	152

Tibia.

Greatest length	160 mm.
Transverse diameter of proximal end	143
Transverse diameter of median region	64
Transverse diameter of distal end	103

Fibula.

Greatest length	157
Transverse diameter of proximal end	82
Transverse diameter of median region	78
Transverse diameter of distal end	132

Mesopodial (?).

Anteroposterior diameter	46
Transverse diameter	42

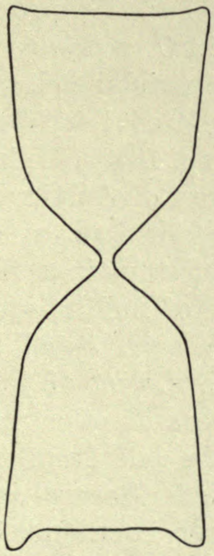
CYMBOSPONDYLUS PISCOSUS Leidy.

Cymbospondylus piscosus Leidy, Proc. Philad. Acad. Sc., 1868, vol. 20, p. 178.
Cymbospondylus piscosus (Merriam), Univ. Calif. Publ., vol. 3, p. 104.

Anterior and posterior faces of dorsal vertebral centra deeply and regularly concave from the periphery to the center of the face. Length of dorsal vertebral centra equaling more than half of the height.

Known only from a single specimen found in the Middle Triassic near New Pass, about thirty miles west of Austin, Nevada.

This species is known only from a single specimen consisting of one nearly complete dorsal vertebra with parts of four others. No similar material has been observed in the collections from the West Humboldt Range, and a careful examination of the type locality has not resulted in the discovery of other specimens.



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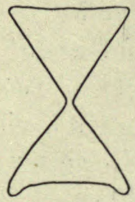

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Fig. 135. *Cymbospondylus petrinus* Leidy Anteroposterior section of a middle or anterior dorsal vertebra, × ¾.

Fig. 136. *Cymbospondylus piscosus* Leidy. Anteroposterior section of an anterior or middle dorsal vertebra, × ¾.

The characters of *C. piscosus* differ from those of *C. petrinus* and *C. nevadanus* sufficiently to warrant specific separation. As far as this form is known, there seems to be no reason for making a generic separation between it and the better known *C. petrinus*.

The vertebrae which are present in the type specimen (fig. 137) represent an individual smaller than the average of *C. petrinus* or of *C. nevadanus*. They belong in the anterior or middle dorsal region, as the parapophyses have disappeared and the diapophyses are elongated inferiorly. The upper arches are thicker than in *Ichthyosaurus,* and the zygapophyses are large.

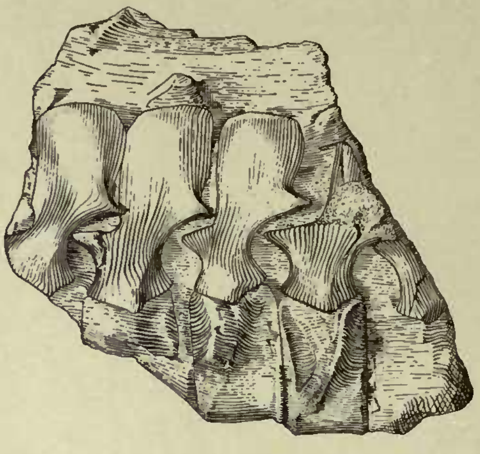

Fig. 137. *Cymbospondylus piscosus* Leidy. Lateral view of type specimen, × ½.

CYMBOSPONDYLUS NEVADANUS, n. sp.

Represented only by individuals of larger size than the average of known specimens of *C. petrinus*. Epipodials (?) of posterior limb much shorter and more massive than in *C. petrinus*. Tibia (?) very short and thick; distal end not narrower than proximal end, and without the flat anterior face present in *C. petrinus*. Middle caudal vertebrae high and narrow.

Type specimen, no. 10620, Univ. Calif. Col. Vert. Palae. (pl. 13), from New Pass, thirty miles west of Austin, Nevada.

In the summer of 1906 an expedition to New Pass, Nevada, visited the outcrops of Triassic limestone in that region, and made careful search for saurian remains in the hope of finding satisfactory material corresponding to Leidy's *Cymbospondylus piscosus*. Small limestone outcrops were found near the pass, and about three miles west of the New Pass mines. They are so distinctly set off from the areas of other rocks that there can be little doubt that the locality visited is the one from which Leidy's specimen of *Cymbospondylus piscosus* was obtained. Several isolated fragments of vertebrae and ribs were obtained; and one specimen (no. 10620) including a number of anterior caudal vertebrae, fragments of ribs, and several elements of the posterior limbs was found in place in the limestone. All of the saurian material from the New Pass limestones seemed to come from a single stratum about three feet in thickness. No new material was found which can be referred to *Cymbospondylus piscosus*. The Triassic limestones at the New Pass locality are stated by Professor James Perrin Smith to be of nearly the same age as the Middle Triassic horizon of the West Humboldt Range.[55]

The best specimen (no. 10620) consists of ribs, caudal vertebrae, and the epipodial limb elements, which were discovered in place in the limestone. Its characters differ from those of typical *C. piscosus* and *petrinus* of the type localities, and it appears to be necessary, for the present at least, to consider it as a distinct species. The lateral apophyses of the caudal vertebrae present are reduced to small rounded projections situated a short distance below the middle of the sides of the centrum. The vertebrae may be considered as representing the anterior or middle portion of the caudal region. The centra are considerably higher than wide and their anteroposterior diameter is relatively short. The anterior and posterior faces are so deeply concave that the central partition is almost if not quite broken through. The concave faces show a little peripheral flattening, but the sharpness of the concavity in the middle portion is not greatly in excess of that near the marginal area.

An upper arch associated with a centrum is considerably flattened laterally, though the summit of the blade is quite thick. The thickness is, however, nearly uniform for almost the whole of the anteroposterior diameter of the summit of the dorsal spine or blade. The summit is excavated or deeply pitted. The zygapophyses are much like those in the anterior portion of the caudal region of *C. petrinus*.

MEASUREMENTS OF A CAUDAL VERTEBRA, NO. 10620.

Height of centrum	138 mm.
Transverse diameter of centrum	104
Anteroposterior diameter of centrum	53
Height of an upper arch	85
Anteroposterior diameter of an upper arch	52
Thickness of an upper arch at summit	18

Accompanying the vertebrae in specimen 10620 there are several ribs. They are round in cross-section near both the proximal and distal ends. The shaft increases in diameter very considerably at the rib head, but does not show much lateral compression. The articular face appears to be hollowed out to a considerable extent.

Associated with the ribs and vertebrae of no. 10620 there are two bones (pl. 13, figs. 4*a* and 4*b*) which do not correspond exactly in form to any elements that have been seen in other material thus far examined. They are elongated, with a long diameter a little less than the height of the vertebral centra. The middle portion is very slender, with a nearly round cross-section, and a diameter equaling about one-sixth of the length. Both ends are much

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[55] See list of species, p. 19.

expanded, one being nearly round and apparently deeply hollowed terminally. The other end is broadened and is considerably flattened in a plane standing almost at right angles to a less pronounced plane of compression of the opposite termination. These elements may represent caudal ribs from a region somewhat farther back in the series than the location of the more elongated and evenly rounded ribs described above. The less compressed end of the shorter bones corresponds quite closely with the proximal termination of the certainly known ribs described above, and is also somewhat smaller than the heads of these ribs. The flattened and expanded end may represent a modification in the terminal portion of a sacral rib, or may be the normal form in all anterior caudal ribs.

With the vertebrae and ribs of this specimen (10620) there are two elements, one of which (pl. 13, fig. 2) represents either a propodial or an anterior epipodial element of the posterior limb; the other (pl. 13, fig. 3) is either a posterior epipodial element of the hind limb or the ischial element of the pelvic arch. The first mentioned bone is much less elongated than either the femur or the tibia of *Cymbospondylus petrinus,* and is most nearly comparable with the tibia of *Shastasaurus* or *Delphinosaurus.* As there is no trace of a proximal trochanteric elevation, though the bone is perfectly preserved, it may, presumably, be considered as the preaxial, epipodial element, but of a type quite different from that seen in *C. petrinus.*

The other bone has almost the same axial diameter as the element referred to as the tibia, but is considerably thinner, particularly at the distal end. This element is slightly constricted medially, and greatly expanded distally. The distal expansion resembles the broadening of the distal end of the fibula in *C. petrinus.* If this element is the fibula, the limb must have been much broader than in *C. petrinus,* and the epipodial region relatively shorter. In any case the limb must have differed quite considerably from that of *C. petrinus,* and suggests a specialization of the epipodial region approaching that of *Shastasaurus.*

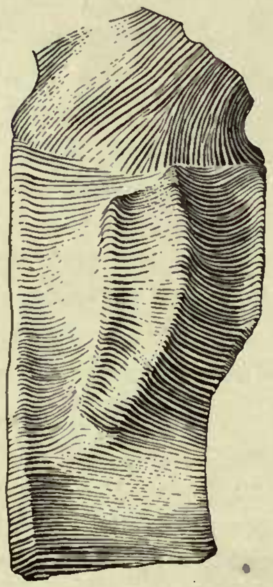


Fig. 138. *Cymbospondylus nevadanus,* n. sp. (?) Lateral view of anterior dorsal vertebra, × ½.

Another specimen (no. 10821) from New Pass, consisting of an isolated vertebral centrum (fig. 138) with a portion of the neural arch attached to it, represents the anterior or middle dorsal region. The centrum is relatively elongated compared with those of the same region in *Shastasaurus,* but does not differ greatly in this respect from the corresponding centra of *C. petrinus.* The anterior and posterior faces are deeply excavated. There is a single rib articulation which extends from the base of the upper arch to a point a little below the middle of the centrum, but the lower end does not swing forward to the anterior margin, as is generally the case in *C. petrinus*. This form can be only tentatively separated from *C. petrinus*, but with the differences shown in the small amount of material available it is not considered advisable to refer it to that species, and it may be referred to *C. nevadanus*.

MEASUREMENTS, NO. 10620.

Posterior dorsal rib.		
Vertical diameter of rib head	60	mm.
Anteroposterior diameter of rib head	36	
Caudal rib?		
Length	130	
Greatest diameter of middle of shaft	21	
Greatest diameter of less compressed end	48	
Thickness of the less compressed end	35	
Greatest diameter of more compressed end	53	
Thickness of the more compressed end	25	
Preaxial epipodial of posterior limb (?).		
Axial diameter	123	
Transverse diameter of proximal end	140	
Transverse diameter of median region	114	
Transverse diameter of distal end	146.5	
Greatest thickness of proximal end	65	
Postaxial epipodial of posterior limb (?).		
Axial diameter	135	
Transverse diameter of proximal end	95	
Transverse diameter of median region	77	
Transverse diameter of distal end	180	
Greatest thickness at proximal end	50	

MEASUREMENTS OF ANTERIOR DORSAL VERTEBRA, NO. 10821.

Height of centrum	110	mm.
Transverse diameter of centrum	110	
Anteroposterior diameter of centrum	64	

TORETOCNEMUS Merriam.

Toretocnemus Merriam, Univ. Calif. Publ. Geol., vol. 3, p. 251, pl. 24.

Vertebral centra relatively elongated. Neural arches not greatly thickened, but showing distinct lateral ridges. Caudal vertebrae with long Y-shaped lower arches. Middle dorsal rib heads sharply divided into lower head and tubercle. Diapophyses and parapophyses of vertebral centra widely separated in the middle dorsal region. Posterior limbs equaling the anterior in size.

Limbs with three digits and a rudimentary fourth. Epipodial segments elongated and enclosing a wide space. Radius with median constriction, ulna notched only on the median border. Proximal row of mesopodial region including only three elements. Carpals and tarsals in linear series. Phalanges generally notched on one or both sides. Ischium and pubis plate-like; pubis very broad, and with obturator foramen. Ilium slender and elongated.

The type specimen, no. 8100, was obtained in the upper portion of the Trachyceras Beds at Bear Cove, on the east side of Brock Mountain, between Pit River and Squaw Creek, Shasta County, California. Other specimens evidently to be referred to this genus are known from the Trachyceras Beds.

Toretocnemus is distinguished from all of the other American Triassic ichthyosaurs by the double rib articulation of the middle dorsal region. (See fig. 59, p. 49.) In the characters of the limbs it has much in common with the genus *Merriamia,* excepting that the posterior limbs are relatively large. The pelvis is more primitive than that of any other Upper Triassic ichthyosaurian. (See fig. 69, p. 55.) It differs from the posterior arches of other Triassic forms, excepting *Cymbospondylus,* in the enclosing of the obturator foramen. The ilium seems to be more slender than in any other known form.

TORETOCNEMUS CALIFORNICUS Merriam.

Toretocnemus californicus Merriam, Univ. Calif. Publ. Geol., vol. 3, p. 251, pl. 24.

The type specimen, no. 8100, Univ. Calif. Col. Vert. Palae., is the only determined material which has been completely exposed for study. A number of other small specimens from the same beds show similar characters. The type specimen was found embedded in a thin slab of shaly limestone which had been weathered in such a manner as to destroy a considerable part of the skeleton. The remaining fragments are not far removed from their natural positions. The parts present represent small fragments of the head, a vertebral series extending from the middle dorsal region to the middle of the tail, the pelvis nearly complete, the proximal half of both posterior limbs, a part of an anterior limb, and numerous ribs.

This was the first American Triassic ichthyosaur in which the constricted phalangeal elements (fig. 139) were discovered. In the character of its limbs and pelvis this is the most primitive American Upper Triassic form. Whether the bicipital rib articulation of the middle dorsal region indicates primitive characters may perhaps be open to doubt. It is nevertheless most nearly paralleled by the structure of some

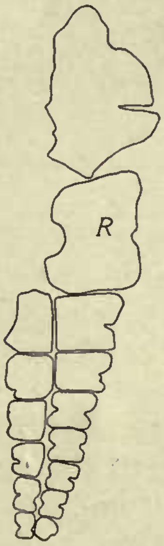


Fig. 139. *Toretocnemus californicus* Merriam. Anterior limb, natural size. *R,* radius.

of the earliest known European forms. The elongated vertebral centra are evidently of a more primitive form than the shorter centra of the shastasaurian type.

MERRIAMIA Boulenger.

Leptocheirus Merriam, Univ. Calif. Publ. Geol., vol. 3, p. 251, May, 1903. Preoccupied by *Leptochirus*.

Merriamia Boulenger, Proc. Zool. Soc. Lond., vol. i, p. 425, Aug. 2, 1904.

Caudal vertebrae with elongated centra. Dorsal ribs single-headed. Coracoid elliptical, without pedunculation or emargination. Scapula with distal expansion and short anterior hook. Posterior limbs much smaller than anterior. Limbs with three digits and a much reduced rudiment of a fourth. Epipodial elements elongated and separated by a wide gap. Proximal row of mesopodial region with three elements, and intermedium supporting but a single element distally. Phalanges generally notched on one or both lateral margins. Angular element of mandible relatively small. Dentition undifferentiated, tooth crowns conical.

The genus is distinguished from *Toretocnemus* by the relatively small posterior limbs, and the single-headed rib articulation of the dorsal region. It differs from *Delphinosaurus* greatly in the form of the known elements of the limbs and of the pectoral arch. *Shastasaurus* represents a type of specialization somewhat similar to that of *Delphinosaurus* but much more extreme. *Mixosaurus* differs very considerably in the whole structure of the limbs, arches, and dentition.

This genus is represented by a single species occurring in the Trachyceras Beds of the Upper Triassic limestones of Shasta County, California.

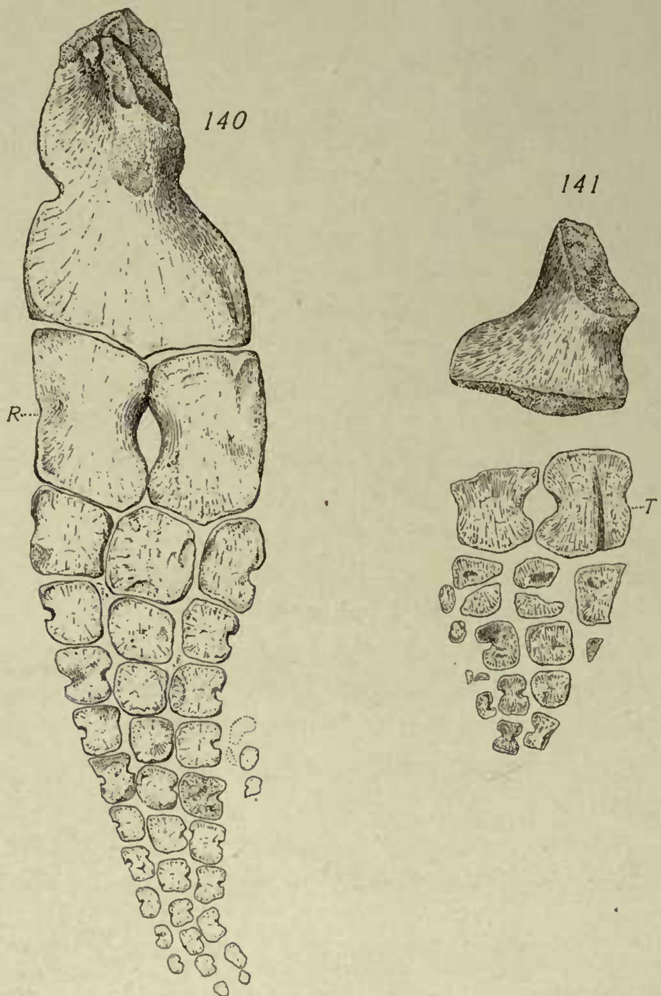
MERRIAMIA ZITTELI (Merriam).

Leptocheirus zitteli Merriam, Univ. Calif. Publ. Geol., vol. 3, p. 253, pls. 21, 22, and 23.

Merriamia zitteli (Boulenger), Proc. Zool. Soc. Lond., vol. i, p. 425. Aug. 2, 1904.

The type specimen, no. 8099, Univ. Calif. Col. Vert. Palae., was found in the Trachyceras Beds of the Hosselkus Limestone at Smith's Cove, between Squaw Creek and Pit River, Shasta County, California. It includes about one-half of the skull, the pectoral arch and limb, a large part of a pelvic limb, with a number of vertebrae, ribs, and abdominal ribs. In this form the tridactyl type of limb is better expressed than in any of the other Triassic forms known (figs. 140 and 141). A somewhat similar form of limb is seen in some of the longipinnate forms of *Ichthyosaurus*, as *I. acutirostris* Owen, *I. platyodon* Conybeare, and *I. tenuirostris* Conybeare.

With the pectoral arch of the type specimen of this species the clavicles were present in front of the coracoids. They are represented by two broad bars of bone meeting or possibly overlapping at the median line. The ends directed toward the scapulae are unfortunately broken away. The median ends are broad and are concave on what appears to be the posterior side. As far as can be determined these elements are much like the clavicles of *Shastasaurus*. An elongated triangular bone situated immediately behind the ends of the clavicles may represent the interclavicle. If this element is represented entire in this specimen, the posterior median arm or stem is very little developed, and is relatively smaller than in any other ichthyosaurian.



Figs. 140 and 141. *Merriamia zitteli* (Merriam). Anterior and posterior limbs, × ½. Fig. 140, anterior limb; *r*, radius; fig. 141, posterior limb; *t*, tibia.

Fig. 142. *Merriamia zitteli* (Merriam). Lateral view of caudal vertebra, × ¾.

A caudal vertebra of this species (fig. 142) shows a considerably elongated form somewhat like that of *Toretocnemus*. The end faces are deeply concave and do not show a peripheral flattening of the face.

DELPHINOSAURUS Merriam.

Shastasaurus perrini Merriam, Univ. Calif. Publ. Geol., vol. 3, p. 89, pls. 5, 6, and 7.
Delphinosaurus Merriam, Amer. Jour. Sc., vol. 19, p. 24, fig. 3. Jan., 1905.

Vertebral centra relatively much elongated, length of dorsal centra equaling one-half to three-fourths of their height. Neural arches of dorsal vertebrae much compressed laterally, though low lateral ridges or ribs are present. Scapula broad sickle-shaped, and without anterior notch or hook. Coracoid not pedunculate, with a well-marked anterior notch. Humerus narrower medially than in *Shastasaurus*. Epipodial elements of anterior limb both relatively elongated, and with median constriction. The genus ranges through the greater part of the lower or shaly horizon of the Hosselkus Limestone.

In the first study of *D. perrini*, the type species of this genus, the vertebrae were distinguished from those of the other forms referred to *Shastasaurus* by their extraordinary anteroposterior diameter. The typical species was, however, referred to the genus *Shastasaurus*, other distinguishing characters not being recognized owing to the fact that excepting ribs and vertebrae nearly all of the parts present in this species were lacking in the known species of *Shastasaurus*. More recent discoveries have made known nearly the whole of the skeleton of this form excepting the distal portions of the paddles. While the skeletal structure obviously represents the shastasaurian group, it is distinguished from that of the typical species of *Shastasaurus* by several important characters other than those of the vertebrae. Only one species, *D. perrini*, is recognized.

DELPHINOSAURUS PERRINI Merriam.

Shastasaurus perrini Merriam, Univ. Calif. Publ. Geol., vol. 3, p. 89.
Delphinosaurus perrini Merriam, Amer. Jour. Sc., vol. 19, p. 24. Jan., 1905.

Type specimen no. 9119, Univ. Calif. Col. Vert. Palae. Since the discovery and description of the type material three valuable specimens representing this species have been obtained. A considerable number of more fragmentary specimens indicate the geologic range of the species.

No. 10998 (pl. 7, fig. 3), a small specimen about two metres long, represents a large part of the skeleton, extending from the anterior region of the skull to the end of the tail. This specimen is somewhat smaller than the type of *D. perrini*, and the vertebral centra are slightly less elongated in proportion to their height, but the resemblance to that species is in general very close. In this specimen the vertebral column includes 115 centra and appears to be nearly complete. About 75 of the centra are in the caudal region, which constitutes nearly one-half of the length of the column. The remaining 40 vertebral centra reach to the posterior part of the skull. Beneath the skull, weathering and imperfect preservation of the bones make it difficult to determine how many centra have been present, but there could hardly have been more than ten, and the number was probably somewhat less. The total number of vertebrae for the presacral region including an estimate of between five and ten for centra possibly lost beneath the skull would be near 45, or about the same as in *Ichthyosaurus.* In the type specimen there are 35 presacrals present, and the estimated number for the whole presacral region is also about 45.

The caudal region of no. 10998 terminates with a series of very small centra about ten millimeters in height. It appears to be nearly complete, though a few more terminal centra may have been present originally. In the distal half of the caudal region, following a slight downward curvature, the tail is bent upward and down again as in *Mixosaurus,* and at the extreme distal portion it is curved upward again. As the whole vertebral column is turned partly over, and is somewhat disturbed in this specimen, it may perhaps be questioned whether the curvature seen here represents the normal position of the vertebral column in the caudal fin. There is, however, relatively less disarrangement of the vertebral centra in the caudal region than elsewhere, and a part of the sinuosity shown may represent a normal vertical curvature, somewhat resembling that of *Mixosaurus.*

In the vertebral column of the type specimen of *D. perrini* there are between 25 and 30 vertebrae in that portion of the caudal region anterior to the bend of the tail. In specimen 10998 the beginning curvature seems to occur between the 25th and 35th caudals.

Throughout the whole vertebral column the centra are extraordinarily long for ichthyosaurians. In a middle dorsal of the type specimen the ratio of height to length is 1:84, and in an interior caudal 1:56.

The spines of the upper arches are not greatly elongated in any part of the column, but are in general considerably compressed laterally (see fig. 32*a* and 32*b,* p. 34), particularly in the dorsal and anterior caudal regions. The strong lateral compression of these arches stands in decided contrast to the wide cross-section of the neural spines of the dorsal region in some forms of *Shastasaurus.* That the flattened form of spine is derived from an originally thicker type, is suggested by the distinct lateral rib situated about the middle of the expanded blade of each arch.

The *rib* articulation is evidently similar to that of *Shastasaurus.* Though little is known of the most anterior cervical vertebrae, they seem to have supported bicipital ribs. From the anterior dorsals back to the caudals the ribs were single-headed. In the posterior dorsal and anterior caudal regions the rib heads are well preserved, and there is no evidence of bifurcation of the heads, as has been suggested for *Mixosaurus.*

In the anterior dorsal region the rib heads articulate mainly upon the large diapophyses, but the upper portion seems to have been distinctly in contact with the base of the neural arch. (See fig. 26, p. 32.) About as far back as the twenty-fifth vertebra the bases of the upper arches are produced laterally over the tops of the centra so that the lateral extremities are immediately over the lateral faces of the diapophyses. The ends of these lateral spines of the neural arches appear distinctly truncated, and the lateral faces were evidently continuous with the articulating faces of the diapophyses.

The rib articulation remains high up on the side of the centrum as far back as the middle of the dorsal region, where it suddenly drops to the middle of the centrum.

In all specimens examined the lower arches of the caudals in this species are very long, while the right and left elements are fused inferiorly to form a spine which may be considerably longer than the V-shaped portion above. The articulation of the lower arches is intervertebral, and pairs of distinct facets are formed on the adjoining margins of the centra with which the arches are in contact.

The long dorsal ribs of *D. perrini* are of the same general form as those in *Shastasaurus,* but do not show as pronounced outward curvature of the upper portion of the articular face as in *Shastasaurus altispinus*. In the dorsal region the rib shaft is furrowed anteriorly and posteriorly for a large part of its length.

The *pectoral arch* was represented in the type specimen by a fragment of a coracoid. In specimen 9082 (pl. 14) the scapula, coracoid and probably the clavicle are preserved. The scapula (fig. 143) differs from that of all other ichthyosaurians in having a broadly sickle-shaped or lunate form without an anterior hook as in most other Triassic forms. The posterior margin is much shorter than the anterior and is strongly concave. It is separated from the proximal and distal margins by sharp angles. The anterior margin is regularly convex, and curves into the proximal and distal margins, from which it is not distinctly separated.

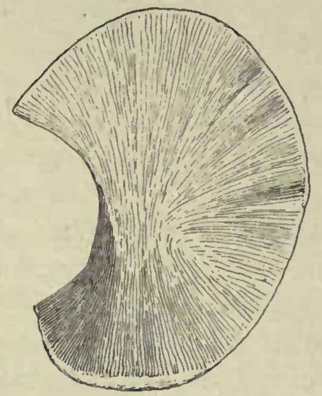
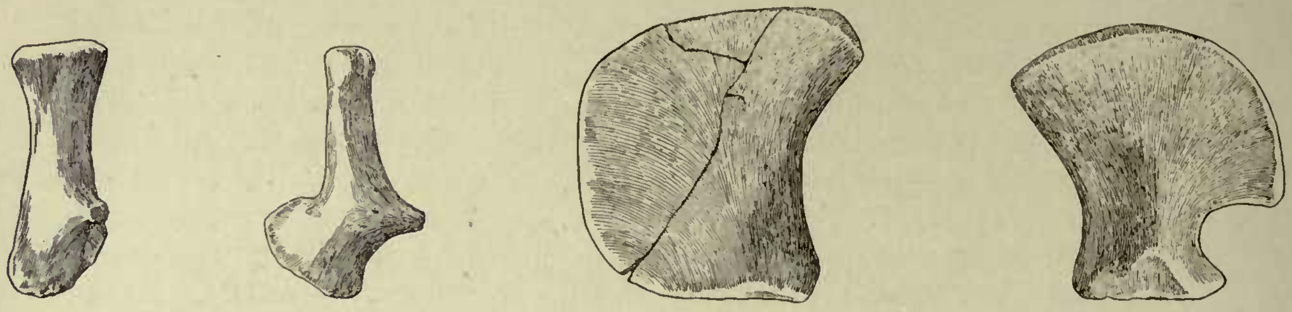


Fig. 143. *Delphinosaurus perrini* Merriam. Scapula, × ¾.

The coracoid has the form of an ellipse with a strong emargination at one end. The general outline is somewhat similar to that of *Ichthyosaurus ingens* Theodori.

Large curved elements which may represent the clavicles are present on the slab in specimen 9082, and are in contact with the scapula. No interclavicle is known.

With specimen 9082 both *anterior limbs* are present with the pectoral girdle (pl. 14), but in both limbs the phalangeal elements have been lost or scattered. The propodial and epipodial segments are different from those of any other known form. The humerus is considerably narrower medially than in *Shastasaurus,* and is much more abbreviated and of very different form from that in *Merriamia* or in *Cymbospondylus.* Excepting *Cymbospondylus,* this is the only known Triassic type in which both epipodials of the anterior limb show a median constriction. The ulna and radius have nearly the same form. In both bones the median border is concave, and the lateral border is deeply notched. Both elements are relatively much longer than in *Shastasaurus,* and approach the length of the humerus.


144a 144b 145 146

Figs. 144*a*-146. *Delphinosaurus perrini* Merriam. Elements of pelvis, × ½.
Fig. 144*a*, ilium, posterior view; fig. 144*b*, ilium, median side; fig. 145, ischium; fig. 146, pubis.

A proximal and a distal row of carpals, including three elements in each row, are present. The proximal row is evidently complete, the same elements appearing in both right and left limbs. The distal row may have included more elements, though they are not represented in this specimen. In the first row the radiale shows an anterior marginal notch as in the longipinnate ichthyosaurs. The intermedium is large and subquadrate in form in both right and left limbs. The ulnare is relatively small and nearly circular in both limbs. In the second row of carpals the third element from the anterior border is almost immediately opposite the ulnare, and shows the same dimensional relations to carpalia one and two that the ulnare shows in relation to the radiale and intermedium. The noticeable reduction of the posterior elements in both rows of the carpus seems to indicate a reduction of the posterior digits equaling or exceeding that in the tridigital manus of the genus *Merriamia.*

The rounding of the margins of the carpal elements evidently indicates the presence of considerable cartilage, and suggests a fairly high stage of specialization.

The elements of the *pelvis* are all shown in the type specimen (pl. 17, and text-figs. 144 to 146). An ischium and a pubis of similar character are also present in specimen number 9086. The determination of these bones was to some extent tentative in the study of the first specimen, but seems now fully justified by what is known of the pelvis of other Triassic ichthyosaurians in which the position of the elements is definitely determined. The pelvic bones are in general much like those of *Shastasaurus*. The ilium is distinguished from that of all the other Triassic genera by the presence of a tubercle near the outer side of the proximal end. This tuberosity is indicated on both of the known specimens, and has not thus far been seen in any other form. The ischium is somewhat broader than in *Shastasaurus*. In the pubis the proximal end is not as wide as in *S. pacificus*, while the distal hook is not as strongly curved as in that form.

The *posterior limb* (fig. 147) shows much the same stage of development as the posterior one in *S. osmonti* (no. 9608; see figs. 100-101, p. 66). The femur is more distinctly abbreviated than in *Cymbospondylus*, and is somewhat broader than in *S. osmonti* (no. 9608). The tibia and fibula both show a median constriction. The tibia is much larger than the fibula and has nearly the same width at the two ends. The fibula is expanded at the distal end, but as in *Cymbospondylus* the proximal end is barely wider than the middle of the shaft. Several discoidal limb elements are present with the hind limb of the type specimen, but it is uncertain whether they represent mesopodial or phalangeal elements.

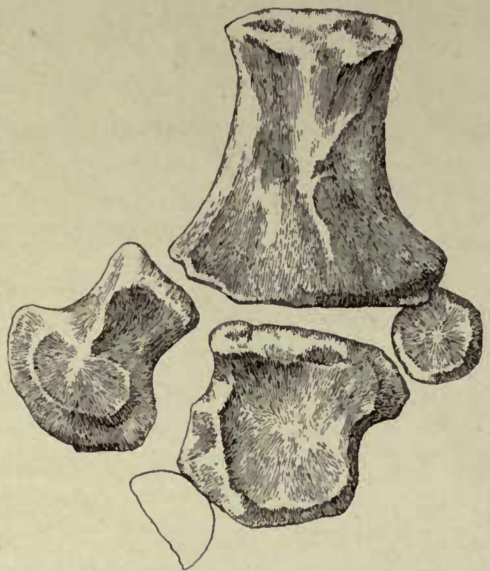


Fig. 147. *Delphinosaurus perrini* Merriam. Posterior limb, × ¾.

A considerable part of the *skull* is present with specimen 10998, and a portion of the cranium with specimen 9082, but as yet it has not been possible satisfactorily to free the delicate bones from the hard matrix.

Of specimen 9082 there are given below the measurements of three anterior dorsal vertebrae, which correspond in their position to about the 15th, 16th, and 17th in the vertebral column; a fourth is near the position of the 25th vertebra.

MEASUREMENTS, SPECIMEN 9082.

15th vertebra, anteroposterior diameter of centrum	21.3 mm.
15th vertebra, height of centrum	30
15th vertebra, height of upper arch	41

16th vertebra, anteroposterior diameter of centrum	21.5 mm.
16th vertebra, height of centrum	30
16th vertebra, width of centrum	33.5
17th vertebra, anteroposterior diameter of centrum	21.5
17th vertebra, width of centrum	33.5
25th vertebra, anteroposterior diameter of centrum	24
25th vertebra, height of centrum	30
25th vertebra, width of centrum	45
25th vertebra, height of upper arch	41

MEASUREMENTS, SPECIMEN 9086.

Anterior caudal vertebra, anteroposterior diameter of centrum	28 mm.
Anterior caudal vertebra, transverse diameter of centrum	*a* 48
Anterior caudal vertebra, height of centrum	52
Anterior caudal vertebra, height of upper arch	48
Anterior caudal vertebra, length of chevron	72
Anterior caudal vertebra, length of stem of chevron	39
Ilium, greatest length	55
Ischium, greatest length	61
Ischium, greatest width	56

a Approximate.

VERTEBRAE OF SPECIMEN 10998.

Number of vertebra counted from anterior end of column*	Height of centrum	Transverse diameter of centrum	Antero-posterior diameter of centrum
3	27mm.		
9			18
20			22
23	35		
36	36		
38		21	
48	33		16
65	23		9
70			
84	19		9
105	16		4.5
110	*a*12		4.5

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* To the number of vertebrae behind the skull about 5 to 10 vertebrae should be added to compensate for a number which have been lost from the anterior end of the column.

SHASTASAURUS Merriam.

Shastasaurus Merriam, Amer. Jour. Sc. 1895, vol. 4, p. 56.
Shastasaurus (Dames), Sitzb. d. Acad. d. Wiss. Berlin, 1895, p. 1048.
Schastasaurus (Boulenger), Zool. Record. Rept. p. 29, 1896.
Schastasaurus (Yakowlew), Verh. d. Kais. Russ. Min. Ges. Bd. 40, p. 194.

Vertebral centra relatively short, neural spines often greatly thickened. Bicipital ribs only in anterior part of series. Coracoid pedunculate; scapula expanded distally, and with anterior hook. Pubis and ischium much expanded distally, pubis with deep obturator notch. Propodials and epipodials of anterior limb relatively much shortened. Epipodial elements separated by a cleft excepting in extreme cases of shortening (*S. careyi*). Posterior elements of epipodial and mesopodial series relatively reduced.

Typical species, *S. pacificus,* from the upper portion of the Trachyceras Beds of the Hosselkus Limestone of Shasta County, California.

This genus is characterized by the extreme specialization of the limbs and of the neural vertebral arches. Both propodial and epipodials of the anterior limb are greatly shortened, the most extreme form appearing in *S. careyi,* where the length may not amount to more than 75 per cent. of the width. With the reduction in length of these elements there has occurred also a reduction of the posterior elements of the limb, so that the posterior epipodial and probably the third or posterior mesopodial were much smaller than in the other genera. Judging from what is known of this reduction, the posterior digit has also suffered reduction, and the limb may have been reduced nearly to a two-fingered type. The elements of the arches are generally thick and heavy. Particularly is this true in the case of the coracoid, which is also exceptionally narrow anteroposteriorly near the proximal end.

The skull is fairly well known in this genus, but has not shown any very marked characteristics.

The species occur in the Hosselkus Limestone of Shasta County, California, ranging from the lower part of the Trachyceras Beds to the massive upper limestones. *S. osmonti* seems to range from the Trachyceras Beds, where it is common, to the upper, massive limestone where it is rare. *S. alexandrae, S. altispinus,* and *S. pacificus* are known from the upper portion of the Trachyceras Beds. In the upper, massive limestones *S. careyi* is the common form, vertebrae of *S. osmonti* being seen with it occasionally. *S. caryei* may possibly occur also in the upper part of the lower horizon.

The history of the genus seems to show pretty clearly a gradual evolution out of an earlier, smaller, and less specialized type like *S. osmonti,* to the much larger and more highly specialized *S. careyi,* which is almost the only form seen in the upper, massive limestones.

As yet no true *Shastasaurus* is known from the Middle Triassic formation of Nevada.

From the evidence of a very small quantity of fragmentary material it appears possible that ichthyosaurian forms at least allied to *Shastasaurus* have had a wide geographic distribution in Triassic times. From an examination of the measurements of Hulke's *Ichthyosaurus polaris* the writer has suggested (1902, 2, p. 88) that this form closely resembles in character the posterior dorsals of *Shastasaurus*. More recently Yakowlew (1902, 1, p. 194) has described additional material from this region. This he refers to the species *polaris*, which is considered by him to be a true *Shastasaurus*. As is indicated elsewhere (p. 150) this form is possibly nearer to *Cymbospondylus* than to *Shastasaurus*.

SHASTASAURUS OSMONTI Merriam.

Shastasaurus osmonti Merriam, Univ. Calif. Publ. Geol., vol. 3, p. 93, pls. 8, 9, 10, and 11.

Vertebral centra relatively longer than in *S. careyi*, and somewhat shorter than in *S. pacificus* or *altispinus*. Neural arches of dorsal vertebrae showing more lateral compression than *S. careyi* and *altispinus*. Coracoids and humerus much broader and thicker than in *S. alexandrae*. Humerus less abbreviated than in *S. careyi*.

This species was the first American Triassic ichthyosaur of which enough material was found to make possible a satisfactory determination of its systematic position. The type specimen consisting of thirty-five vertebrae from the anterior portion of the column, together with the most important elements of the anterior arch and limb, was obtained by Mr. V. C. Osmont from the Atractities Beds of the Hosselkus Limestone, at Smith's Cove, on the west side of Brock Mountain, between Squaw Creek and Pit River, in Shasta County, California. Several other specimens representing about as large a portion of the skeleton as the type, also many isolated bones or small parts of skeletons, have been obtained. The species ranges from well down in the Trachyceras Beds of the lower or more shaly division of the Hosselkus Limestone up into the higher, massive, gray limestone horizon represented in part by the Spiriferina Beds. It is most common in the upper part of the lower or more shaly division.

The species includes individuals probably ranging from 12 to 18 or 20 feet in length.

In the type specimen, no. 9076, Univ. Calif., Col. Vert. Palae., a series of vertebrae shows the characters of the centra from the axis to the 36th centrum. (See fig. 57, p. 48.) As far back as this series of centra extends the faces of articulation of the diapophyses are confluent above with the articular faces for the neural arches. In the anterior region of the column the diapophyses are relatively short, and well developed parapophyses are present below them. In proceeding backward in the series the diapophyses gradually elongate, and in the middle dorsal region develop a knee-like bend at about the middle of their height, the lower portion of the apophysis swinging forward almost to the anterior margin of the centrum. Behind the anterior ten or eleven vertebrae the parapophyses are reduced and were not functional. The last minute trace appears on one side of the eighteenth centrum.

The upper arches of the vertebrae in the most anterior cervical region possess slender spines with a round cross-section. The spines of the dorsal arches are thick compared with those of *Ichthyosaurus,* but they are more compressed laterally than in *S. altispinus* or *S. careyi.*

The ribs are rather heavy and tend to develop the outward curvature of the upper portion of the articular face, permitting a rocking movement, but much less strongly than in *S. altispinus* (see figs. 66*a* and 66*b,* p. 52) or *S. careyi.*

In specimen 9081 there is present the posterior portion of a cranium of *S. osmonti* with the cervical and anterior dorsal vertebrae, the pectoral girdle, and portions of both anterior limbs. The limb and arch elements are slightly smaller than those of the type specimen, but the general form and proportions are the same. In this specimen the series of cervical vertebrae seems to be complete, though the anterior individuals are displaced somewhat. Immediately behind the articular face of the basioccipital is a small, thin centrum representing the atlas. One surface shows a funnel-like concavity which extends inward almost from the margin. The opposite side is gently convex, excepting a small, shallow, central concavity covering not more than one-third of the area. The widely concave side apparently represents the posterior face, the anterior face of the centrum considered as the axis being also deeply concave. Its funnel-shaped form is, moreover, not the form of excavation that would probably develop in articulation with the basioccipital. The posterior articular face of the basioccipital is strongly convex, and the middle of the face evidently rested in the small concave middle area of the anterior side of the atlas.

The atlantar centrum differs from that of *Cymbospondylus* in the development of the slight concavity on the otherwise convex anterior face, and in the apparent absence of distinctly marked lateral faces. The addition of a certainly known atlas to the vertebral series of *Shastasaurus* suggests that, as indicated in the original description, the number of cervicals with attached intercentra may be larger than in *Ichthyosaurus.*

A valuable specimen (no. 9608; pl. 17, fig. 1) found during the season of 1903 appears to correspond to *S. osmonti,* and shows the previously unknown vertebrae and ribs of the posterior dorsal, sacral, and anterior caudal regions, together with all of the pelvic elements, and the first two segments of the posterior limb.

Over thirty vertebrae are present with this specimen, the number being about evenly divided between presacrals and postsacrals. They have been but little disturbed, but are so turned that measurements of their height cannot be made in most cases without destroying neural arches or ribs. The length and height of a dorsal about fifteen vertebrae in front of the pelvis are nearly the same as in the type specimen of *S. osmonti.* The anterior caudals are much shorter than the corresponding centra of *D. perrini.* A comparison of the vertebrae of this form with *S. pacificus* is difficult, as the portion of the vertebral column represented in that species is here covered by the ribs. The neural spines of the most posterior dorsals are, however, much like those in the type specimen of *S. pacificus.* The pelvis so far as known is quite different from that of *S. pacificus.*

Short caudal ribs and long-spined Y-shaped chevrons are present on the anterior caudal vertebrae.

MEASUREMENTS OF VERTEBRAE, SPECIMEN 9608.

Anteroposterior diameter of the centrum of a posterior dorsal about fifteen vertebrae in front of the pelvis	32 mm.
Height of 15th centrum in front of pelvis	69
Height of a neural arch about seven vertebrae in front of the pelvis	66
Anteroposterior diameter of an anterior caudal centrum immediately behind the pelvis	32
Height of neural arch of anterior caudal immediately behind the pelvis	52
Length of an anterior caudal chevron	[a] 114

[a] Approximate.

The coracoid of the type specimen of *S. osmonti* is characterized by its thickness, and the extreme narrowness of the proximal portion. The form of the scapula is much like that in some mosasaurian genera. The greatly abbreviated and thickened elements of the anterior limb, though shorter and thinner than in *S. alexandrae,* are easily distinguished from the corresponding elements of *S. careyi,* which are much more specialized in these particulars.

Near the humerus in specimen 9081 is a row of three paddle bones from the mesopodial or phalangeal region (pl. 15, fig. 4). Two of them are of nearly equal size, and the third element, at one end of the row, is much smaller. As has been stated elsewhere (p. 72) there is reason to suppose that the relatively large size of the anterior elements of the limb was accompanied by reduction of the posterior elements to such an extent that the limb came to have only three digits, the most posterior of which was relatively small.

Other discoidal paddle bones are present with specimen 9081, and in one of these the margin is distinctly pitted and grooved (pl. 15, fig. 3).

The pelvic elements seen in specimen 9608 (pl. 16) are much like those of *Delphinosaurus perrini,* though the pectoral arch is very different. The ilium is more robust than in *Toretocnemus.* The proximal end is broadened transversely much as in *Delphinosaurus* and *Cymbospondylus.* There is no evidence indicating the presence of a posterior tubercle such as seems to be present on the ilium of *Delphinosaurus.*

The ischium is a broad, plate-like element, but is not as wide as in *Delphinosaurus* or in *Cymbospondylus petrinus.*

The pubis is intermediate in form between that of the *S. pacificus* and the corresponding element of *D. perrini.* It differs from the pubis of *S. pacificus* in the form of the posterior portion of the proximal end, which in *S. pacificus* curves inward and forward toward the posterior hook of the expanded distal portion. In the type specimen of *S. pacificus* the proximal end is broader and the posterior proximal hook more pronounced than in specimen 9608.

Of the left hind limb (pl. 16, fig. 6) the elements belonging to the propodial and epipodial segments are but little disturbed. The femur is a short robust bone with a well developed trochanteric ridge, and a somewhat expanded distal end. It is a little more slender than in *D. perrini,* but is not more elongated than in *Ichthyosaurus.* It is relatively heavier and broader than in *Cymbospondylus.*

Each of the epipodial elements shows a median constriction, and they are in consequence of this separated by a wide gap. The tibia is much larger than the fibula, and is almost equally expanded at the two ends. The fibula is much expanded distally, while the proximal end is hardly broader than the median portion of the shaft. The characters of the epipodial elements are in general much like those of *Delphinosaurus perrini* excepting that both elements are a little more slender than in that form. With the determinable limb bones of this species are several discoidal limb elements which may represent tarsals or possibly phalanges. In one of these rounded elements the thickness of one side is much greater than the other, probably indicating its position near the border of the limb, and the peripheral surface is distinctly concave.

MEASUREMENTS OF SPECIMEN 9608.

Pelvic Elements.	
Ilium, length	110 mm.
Ilium, transverse diameter of distal end	60
Ischium, length	109
Ischium, greatest width	85
Pubis, length	120
Pubis, greatest width of distal blade	105
Pubis, width of proximal end	67

Posterior Limb.

Femur, length	132 mm.
Femur, width of proximal end	78
Femur, greatest diameter of proximal end	84
Femur, width of distal end	117
Tibia, length	96
Tibia, width of proximal end	92
Tibia, width of narrowest portion of shaft	66
Tibia, width of distal end	108
Fibula, length	94
Fibula, width of proximal end	41
Fibula, width of distal end	86

Of the skull only the most posterior portion of the cranium and of the lower jaw are present in specimen 9081. In the posterior parietal region the relations of the parietals are seen for the first time in *Shastasaurus,* the posterior arms of the parietals extending backward behind the parietal arch of the squamosal, as in *Cymbospondylus* and *Baptanodon.*

The relations of the temporal, supratemporal, postorbital and quadrate are distinctly shown, and are much as in *S. alexandrae.* The articular face of the quadrate shows a weak transverse groove.

The form of the basioccipital appears to be different from that in *Ichthyosaurus* or *Baptanodon.* The inferior side of this element is produced as two prominent hypapophyses not unlike the corresponding prominences in *Cymbospondylus* or in the Mosasauria. The posterior articular face is strongly convex.

SHASTASAURUS ALEXANDRAE Merriam.

Shastasaurus alexandrae Merriam, Univ. Calif. Publ. Geol., vol. 3, p. 96, pls. 12 and 13.

Vertebral centra much as in *S. osmonti,* but much longer anteroposteriorly than in *S. careyi.* Anterior cervical ribs double-headed; posterior cervical or anterior dorsal ribs single-headed. Elements of the pectoral arch and anterior limb much broader and thinner, and anterior notch of the humerus much wider than in *S. osmonti.*

Type specimen, no. 9017, Univ. Calif. Col. Vert. Palae., from the upper part of the Trachyceras Beds of the Hosselkus Limestone, one-quarter of a mile south of Smith's Cove, Brock Mountain, between Squaw Creek and Pit River, Shasta County, California. Fragmentary material apparently belonging to this species has been found at other localities in this region.

The type specimen of this species represents an individual of nearly the same size as the type of *S. osmonti,* but the cervical and anterior dorsal vertebral centra are relatively a little longer than in that species. The coracoid, scapula and humerus are all much broader and thinner than the corresponding bones in *S. osmonti.* Though the two species are closely related, the differences are of sufficient magnitude to deserve recognition in an attempt to express in a classification the amount of variation in this genus.

The type specimen is the only individual of a typical *Shastasaurus* of which any considerable portion of the skull is known. Most of the elements are shown in this specimen excepting the rostral region. The cervical vertebral series is complete, and the elements which are of importance in determining the nature of the change in the rib articulation from double to single have been almost perfectly preserved.

SHASTASAURUS PACIFICUS Merriam.

Shastasaurus pacificus Merriam, Amer. Jour. Sci., 1895, vol. 4, p. 56, figs. 1 and 2. Univ. Calif. Publ. Geol., vol. 3, p. 102, pl. 14, figs. 1 and 2, text-fig. 1.

The type specimen of this species, constituting also the type of the genus *Shastasaurus,* was unfortunately represented by only a few posterior dorsal vertebrae and ribs, with one complete pubic bone and a portion of another. Though a considerable quantity of ichthyosaurian material has been known from the Upper Triassic of America, no other specimens have been discovered which seemed certainly to represent this specific type.

The species seems to be characterized by greater length of the vertebral centra anteroposteriorly than in any other species of *Shastasaurus.* The neural arches of the posterior dorsals are short and are considerably thickened but do not show the characters of *S. altispinus* or *S. careyi.*

The form of the pubis (fig. 148) is most nearly approached in *S. osmonti.* It differs from the form in that species in that the proximal end is broader and the posterior portion curves forward and inward toward the prominent posterior hook. In *S. osmonti* the proximal end of the pubis is narrower and is not upturned.

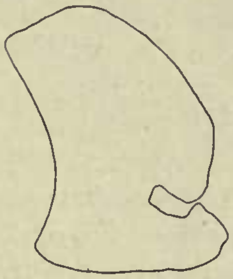

Fig. 148. *Shastasaurus pacificus* Merriam. Pubis, about ¼ natural size.

Associated with the type specimen of *S. pacificus* are three large discoidal elements, similar to those with the posterior limb of specimen 9608, referred to *S. osmonti.* They appear to have been slightly concave on the upper and lower surfaces. The discs are quite thick, and the edges are concave with an uneven or pitted surface. The form of these elements indicates that they were separated by a considerable body of cartilage. The discs resemble the phalanges of *Baptanodon,* but fail to show even the tendency to angularity seen in the proximal mesopodials of that form. Inasmuch as elements of this character are also found associated with the epipodial region in the types of *S. osmonti* and *D. perrini,* it is possible that they are proximal mesopodials. In *D. perrini* (no. 9082), the anterior and middle proximal carpals are however slightly angular. It is not improbable that in this species as in other forms of *Shastasaurus* the mesopodial and phalangeal elements were all reduced to the peripherally grooved or pitted discoidal form.

Though the characters of this form of *Shastasaurus* approach those of *S. osmonti,* and it may ultimately be necessary to unite them, no intermediate types are known. As long as the two forms can be distinguished the interests of classification are best subserved by recognizing them as distinct.

SHASTASAURUS ALTISPINUS Merriam.

Shastasaurus altispinus Merriam, Univ. Calif. Publ. Geol., vol. 3, p. 99, pl. 14, fig. 5, and pl. 15.

Vertebral centra not differing greatly in form and proportions from *S. osmonti;* neural spines of dorsal vertebrae very thick transversely. Excepting the blade-like anterior and posterior margins, they are nearly circular in cross-section. Distal end of spines hollowed by a groove-like anteroposterior excavation. Heads of dorsal ribs with two faces sharply turned away from each other; upper face usually more noticeably pitted than lower. The known podial limb elements with rounded and excavated or deeply pitted margins, but with a distinct notch on the outer side.

Very little is known of this species excepting the type specimen and a small amount of fragmentary material which may belong here. It seems to be fairly distinctly separated from *S. osmonti* and *S. alexandrae* with shorter and broader neural spines and less specialized rib heads. In *S. altispinus* the upper arches of the middle dorsal vertebrae are more than 20 per cent. higher than the centra, and in *S. osmonti* they are 10 per cent. shorter than the centra.

In *S. altispinus* the peculiar double facetted character of the heads of the dorsal ribs seems to be more strongly expressed than in any of the other species (pl. 18, figs. 3*a* and 3*b*). The lower face is generally less distinctly pitted than the upper, and was evidently in direct contact with the lower portion of the diapophysis. The upper face may be turned away from the lower face as much as thirty-five degrees. The surface of the upper face is generally quite distinctly concave. As is shown under the general discussion of the rib articulation of Triassic Ichthyosauria (p. 52) the adjustment of the rib to the vertebral centrum is in these forms quite different from that of the typical *Ichthyosaurus*.

From *S. careyi* this species differs in having longer vertebral centra and very much longer neural vertebral spines, with anteroposteriorly grooved instead of strongly convex terminal faces of the neural spines. The upper ends of the neural spines of the middle dorsal region are also much thicker than the middle portion of the arch in *S. careyi*. In *S. altispinus* a tendency to thicken the upper portion of the neural spines appears, but it is not developed as far as in *S. careyi*.

Two paddle elements occurring with the type specimen of this species both show sharp marginal notches (fig. 149) such as are not seen in any discoidal limb bones of *S. osmonti*. The peripheral face in these elements is concave and much roughened.

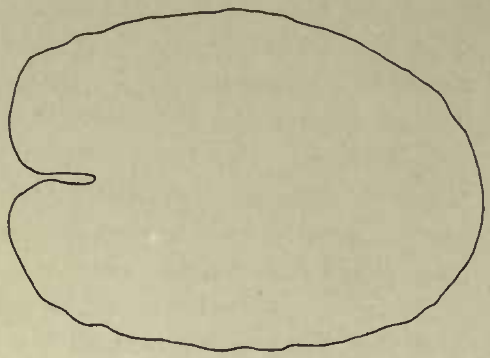

Fig. 149. *Shastasaurus altispinus* Merriam. Marginal element from mesopodial, metapodial, or phalangeal region, × ⅔.

SHASTASAURUS CAREYI Merriam.

Shastasaurus careyi Merriam, Univ. Calif. Publ. Geol., vol. 3, p. 98, pl. 14, figs. 3 and 4.

Vertebral centra relatively high and short. Neural spines of dorsal vertebrae considerably thickened distally. Limb elements more abbreviated than in other species. Radius relatively large.

The type specimen (no. 9075, Univ. Calif. Col. Vert. Palae.) of this species consisted of two very large vertebrae and some rib fragments from the anterior dorsal or posterior cervical region. The diapophyses are short, and rudimentary parapophyses are present below them. The centra are relatively short anteroposteriorly. The dimensions of the centra in this specimen indicate that this form approached the size of the largest known species in the genus *Ichthyosaurus*.

Measurements, no. 9075.

Width of vertebral centrum from anterior dorsal or posterior cervical region	180 mm.
Height of centrum	[a]160
Anteroposterior diameter of centrum	60

[a] Approximate.

A specimen (no. 9614; pls. 15 and 18) obtained from the Upper Triassic of Shasta County, California, in 1903 shows several characters of limbs and vertebrae not previously seen in any of the material from this region. It represents a large animal with greatly abbreviated propodial and epipodial limb elements. The vertebral centra are unusually short anteroposteriorly, while the short neural spines are nearly round in cross-section, and are much swollen at the distal end.

The characters of the limb elements (pl. 15) resemble somewhat those in *S. osmonti.* The humerus is much shorter and broader than in that species and is altogether the most abbreviated proximal limb segment known in any ichthyosaurian. The bone is also remarkably thick throughout, although the pectoral ridge shows relatively but little elevation compared with that of *S. osmonti.* The anterior edge is sharply emarginated as in the other species. On the distal end the faces of articulation are not distinctly separated by an angle as in *S. osmonti,* and the surface is considerably excavated. The radius is relatively large compared with the humerus. Both its length and width are greater compared with the corresponding dimensions of the humerus than in the other species. Its length is also less compared with its own width. Excepting the wide but rather sharply marked notch on the anterior margin, the outlines of the bone are gently rounded, in contrast to the somewhat angular form of the radius in *S. osmonti.* The posterior margin of the bone is convex instead of concave as in all other known Triassic ichthyosaurs, indicating the absence of a distinct gap between radius and ulna. Excepting the notched anterior side the whole border of the radius is sharply excavated by a continuous groove running around the margin.

MEASUREMENTS OF LIMB ELEMENTS, SPECIMEN 9614.

Humerus, axial diameter	156 mm.
Humerus, greatest transverse diameter	212
Humerus, greatest thickness of proximal end	138
Humerus, greatest thickness of distal end	90
Radius, axial diameter	126
Radius, greatest transverse diameter	156

In specimen 9614, ten complete vertebrae are present in series, with the upper arches and ribs very little disturbed. The centra are large and are remarkably thin anteroposteriorly (pl. 18, fig. 5*a*). Judging from the position of the diapophyses they belong to the middle dorsal region. The centra are thinner than in any other species of *Shastasaurus,* unless it be *S. careyi.* The diapophyses are long and narrow. The anterior and posterior faces of the centra are evenly but deeply biconcave. The neural arches are relatively short, their height being considerably less than the height of the centra. The distal ends of the neural spines are much expanded and thickened, and the upper portion is slightly domed, instead of excavated as in *S. altispinus.* A horizontal cross-section of the upper portion of the neural spine is nearly circular, and at the upper end of the spine the transverse diameter is considerably greater than the corresponding diameter immediately above the zygapophyses. The zygapophysial facets are well developed although not very large.

MEASUREMENTS OF VERTEBRAE, SPECIMEN 9614.

Height of centrum of vertebra from middle dorsal region	118 mm.
Transverse diameter of centrum	*a*115
Anteroposterior diameter of centrum	34
Length of upper arch	79
Transverse diameter of neural spine behind anterior zygapophyses	25
Transverse diameter of neural spine at upper end	35

a Approximate.

Well preserved ribs (pl. 18, fig. 6) are present with each of the vertebral centra with this specimen. The form of these ribs is in general similar to that of the ribs in *S. osmonti,* excepting that the shaft and head are apparently somewhat heavier. The posterior side of the shaft is strongly grooved in the proximal half. The distal portion has been broken away in all cases. As in *S. osmonti* and *S. altispinus,* the upper portion of the articular face of the rib is turned rather sharply outward from the plane of the lower portion of the face.

Of the known species this form is evidently nearest to *S. careyi* and *S. altispinus.* Though the vertebrae cannot be compared closely with the known type of *S. careyi,* owing to their not belonging in the same region of the column, they seem to be somewhat thinner anteroposteriorly. Their fore-and-aft diameter equals about 29 per cent. of the height of the centrum while in *S. careyi* it equals about 37 per cent.

In *S. altispinus* vertebral centra from a region of the column corresponding closely to that represented in specimen 9614 are much thicker than in this specimen. Also, the neural arches are relatively almost twice as long, and are much less expanded distally.

Considering that specimen 9614 represents a different part of the vertebral column from that seen in the type of *S. careyi,* it is not improbable that it represents the same specific type or at least a closely allied species. The extremely specialized character of the anterior limb found here one would expect to find in *S. careyi* of all the known species, as it is the latest and the largest of the several types.

Mixosauridae of Uncertain Position.

CYMBOSPONDYLUS (?) NORDENSKIÖLDII (Hulke).

Ichthyosaurus nordenskiöldii Hulke, Beihang. K. Svenska Vet. A. Handlingar. Bd. 1, no. 1.

Mixosaurus nordenskiöldii (Dames), Sitzb. der Acad. der Wiss., Berlin, 1895, p. 1047.

To this species Hulke referred a number of vertebrae and ribs obtained by A. E. Nordenskiöld in the Triassic of Saurie Hook, Spitzbergen.

The specimens referred to this species represent a smaller form than *C.(?) polaris.* The vertebrae present represent the thoracic and caudal regions. The dorsal vertebrae (2*a*) described by Hulke are subcircular, slightly angular, and approaching a hexagonal form in anteroposterior profile, the greatest width or transverse diameter nearly equaling the height. The height is about 1.65 in. The anteroposterior diameter is .35 in. They show anterior and posterior articular surfaces which are unequally hollow. On one centrum the diapophysial articular surface is apparently confluent with the neurapophysial articular surface. The interval between the diapophysis and parapophysis exactly corresponded to the interval between the tuberculum and capitulum of a rib near by. As it is described, this vertebra might represent a posterior cervical or an anterior dorsal of either a shastasaurine or an ichthyosaurine form.

The caudal vertebrae referred to this species were recognized by Hulke as differing markedly from the caudals of the typical *Ichthyosaurus,* but their reference to an ichthyosaurian seemed unavoidable owing to their association with unmistakable tabular, polygonal ossicles plainly belonging to an ichthyosaurian paddle. The caudal centra were characterized by having a vertical diameter relatively long as compared with the transverse diameter. The articular faces of the caudals were characterized by a small but deep pit immediately below the middle.

The dimensions of a caudal (series 2, *d* Hulke) were: anteroposterior diameter, .3 in.; vertical diameter, about 1 in.; horizontal transverse diameter, .6 in.

The caudal centra of this species in their general form resemble the centra of the distal third of the caudal region in *Cymbospondylus* (see pl. 9, figs. 8*a* and 8*b*), and of other shastasaurine forms, and do not differ greatly from those of *Mixosaurus.* (See fig. 124, p. 96.)

Two fragments forming part of the snout of a reptile were found by Hulke in the Nordenskiöld collection from Spitzbergen, and were considered as probably belonging in the genus *Ichthyosaurus.* The anterior teeth were smaller than the posterior ones, and were set in an open continuous groove. The posterior teeth were found to occupy separate sockets, the dentary groove being interrupted in this region by transverse partitions between the teeth. All of these teeth showed a simple oblong cross-section through the neck, the anteroposterior diameter being to the transverse as 2:1 or in some cases 2.5:1. A portion of a crown protruding showed relatively coarse longitudinal fluting.

In later examination by Dames (1895) of the specimens studied by Hulke, the statements of Hulke were substantiated, and attention was called to the remarkable similarity of these specimens to *Mixosaurus ?* of the European Middle Trias. Dames noted several minor differences between the dentition of the Spitzbergen form and that of *M.*(?) *atavus*. In *M.*(?) *atavus* the cross-sections of the teeth were stated by Dames to be nearly round, and the partitions between the alveoli weak. In the Spitzbergen form the cross-sections are relatively narrow transversely, and the partitions between the alveoli are strong. According to the observations of the writer the most posterior teeth of *M.*(?) *atavus* may show some lateral compression.

Taking everything into consideration, the affinities of Hulke's *I. nordenskiöldii* seem closer with *Cymbospondylus* than with any other known genus. The Spitzbergen form differs from *Mixosaurus,* particularly in the nature of the rib articulation in the cervical or anterior dorsal vertebrae.

In the great excess of their vertical diameter, the caudal vertebrae of *C. (?) nordenskiöldii* were stated by Hulke to resemble a vertebra found by Sir. Ed. Belcher, in 1852, on Exmouth Island, lat. 77° 16′ N., long. 96° W. This specimen was figured by Owen in the appendix (p. 389) to Belcher's "Last of the Arctic Voyages."

CYMBOSPONDYLUS (?) POLARIS (Hulke).

Ichthyosaurus polaris Hulke, Bihang K. Svenska Vet. Ak. Handlingar, Bd. 1, no. 9.

Ichthyosaurus (Mixosaurus) polaris (Dames), Sitzb. der Acad. der Wiss., Berlin, 1895, p. 1405.

Ichthyosaurus? (Shastasaurus?) polaris (Merriam), Univ. Calif. Publ. Geol., vol. 3, pp. 87 and 88.

Shastasaurus polaris (Yakowlew), Verh. d. Kais. Russ. Min. Ges., Bd. 40, p. 194.

This species was described by Hulke from fragmentary material obtained by A. E. Nordenskiöld in the Triassic of Spitzbergen. Yakowlew (1902, 1) referred a vertebra to this form. Hulke studied two vertebral series. One series included eight vertebrae, the other three. In the series of eight vertebrae the outline of one of the centra is described as roughly that of a rather narrow, long horseshoe. The dimensions of this centrum were as follows: height, 3.9 in.; transverse diameter, 2.7 in.; anteroposterior diameter, 1.4 in. About half way down on the side of one centrum was an oblong rib facet 1.2 in. long and .4 in. wide. The facet was slightly contracted at the middle and extended obliquely downward toward the anterior border of the centrum.

The anterior and posterior faces of the centrum were said to be deeply concave, but relative to the whole area the extent of the concavity was small, and for some distance below the neural canal the surface was nearly plane.

The vertebrae present in the series of eight centra Hulke considered as representing the posterior dorsal or the anterior caudal region. The writer (1902, 2, p. 88) suggested that they resemble the posterior dorsals of *Shastasaurus.* The narrow form of the centra favors somewhat Hulke's suggestion regarding their position in the anterior caudal region, but the long, narrow rib articulation is more like that of posterior dorsals in the shastasaurine group. The limited area of deep concavity on the anterior and posterior faces suggests the characters of *Cymbospondylus petrinus,* in which the posterior dorsals are also relatively narrow (pl. 9, figs. 2 and 3).

The three consecutive centra of the second vertebral series were much compressed laterally and had short rib facets. They may have represented caudals.

Judging from the available material of this species it belongs in the shastasaurine group. It is not possible to make certain of the genus to which it belongs. The suggestion of Yakowlew and the writer regarding its affinities with *Shastasaurus* were justified in the light of the information at hand, but with a better knowledge of the genus *Cymbospondylus* it appears that *polaris* might be placed in that genus with more reason than could be advanced for referring it to *Shastasaurus.*

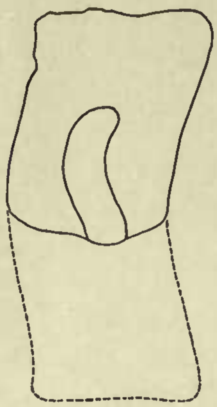
Fig. 150. *Cymbospondylus* (?) *polaris* (Hulke) Middle dorsal vertebra, × ½. (After Yakowlew.)

CYMBOSPONDYLUS (?) NATANS, n. sp.

A perfectly preserved humerus (no. 9873, see pl. 13, figs. 1*a* and 1*b*) from the Triassic of the West Humboldt Range of Nevada differs so much from the humerus of *Cymbospondylus petrinus* that its characters are not covered by the description of that species, and possibly not even by the genus *Cymbospondylus.* In some respects this specimen approaches the genus *Mixosaurus* more closely than does the typical *Cymbospondylus.*

As indicated by the following measurements the humerus is relatively short and broad and represents a somewhat smaller form than the typical *Cymbospondylus petrinus.*

Measurements of humerus, no. 9873.

Greatest length	53 mm.
Greatest width of distal end	38
Width of median or shaft region	31
Greatest thickness of distal end	11

The shaft of the humerus is much shorter than in *C. petrinus*, and is broadened by an expansion of the anterior margin. The posterior half of the proximal end shows a well developed hemispherical articular face which grades into a broad, concave articular face immediately anterior to it. On the anterior side of the lower face of the proximal end there is a short but well marked pectoral ridge. On the distal end, the two articular faces are distinctly separated by a prominent angle. The posterior articular face is much shorter than the anterior. The anterior articular face extends over the anterior distal angle and along the anterior margin for about three-fourths of the distance to the proximal end. The apparent extension of this face over the anterior border probably represents no more than a cartilage covered surface. The anterior articular face is concave transversely and convex in the direction normal to the plane of the distal end. The posterior face is convex transversely and concave in the direction normal to the plane of the end.

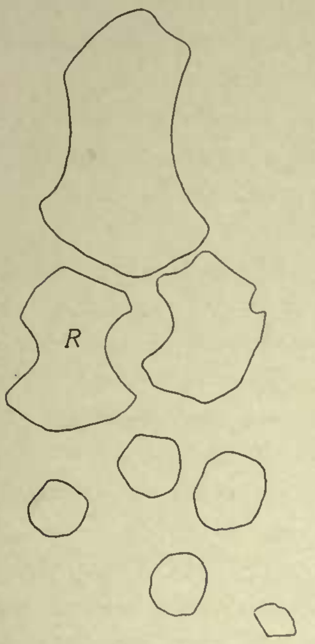

Fig. 151. *Cymbospondylus petrinus* Leidy. Proximal portion of anterior limb, × 1/5.

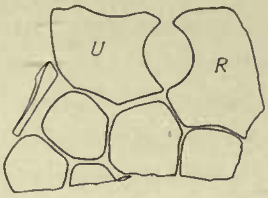

Fig. 152. *Cymbospondylus* (?) *natans*, n. sp. A portion of an anterior limb, × 1/2.

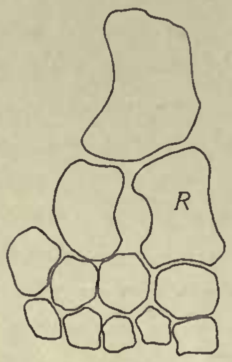

Fig. 153. *Mixosaurus cornalianus* (Bassani.) Proximal portion of an anterior limb, × 1/2. (Adapted from Repossi.)

To this species the writer is inclined to refer tentatively a small specimen (no. 11229; fig. 152) representing a portion of the epipodial and mesopodial region of a limb, accompanied by a number of rather slender ribs. The epipodial elements appear to be less constricted than in *Cymbospondylus petrinus*, and have much the same form as *Mixosaurus cornalianus*. The element which appears to represent the radius was evidently not deeply concave anteriorly, and the ulna was possibly not constricted medially.

The elements of the mesopodial region are angular instead of rounded. There are in the proximal row three elements closely resembling the radiale, intermedium and ulnare of *Mixosaurus*. Behind the ulnare there is a portion of a third element which may represent the pisiform of *Mixosaurus*. Articulating with the ulnare there are two elements in the distal row of the carpus. The anterior of these two shows a small contact with the intermedium. The distal end of the intermedium is not complete.

With this species there may also be placed tentatively several series of caudal vertebrae representing a primitive type of caudal fin. One of these specimens (no. 10624; see pl. 10, fig. 1) is a part of an individual somewhat larger than that represented by the humerus standing as the type of this species. Other specimens showing much the same type of caudal vertebrae as those in no. 10624 belong to smaller individuals.

The vertebral centra in the caudal series mentioned above are high and narrow. They vary somewhat in anteroposterior diameter in different specimens. On specimen 10624 well marked diapophyses are present. The anterior and posterior articular faces are not well shown, but as nearly as can be determined they are not deeply concave from the margins inward, but are probably of the form seen in the caudals of *Cymbospondylus petrinus* (pl. 9, fig. 8*b*).

The upper arches are greatly elongated, the height amounting to more than two and one-half times that of the centrum in one case. Though much elongated the neural arches are not greatly compressed laterally. Zygapophysial notches are noticeable particularly on the posterior margins of these arches.

The lower arches are also very long, their length almost equaling that of the neural arches. Their attachment to the centra cannot be clearly made out in every case. In one instance a suture between an articular head of a lower arch and the centrum can be clearly seen. In other cases the lower arches may possibly be fused with the centra, as in the mosasaurian genus *Clidastes*.

ICHTHYOSAURUS Koenig.

Single articulation of presacral ribs found only in the posterior dorsal region. Hypocentral elements of caudal region not meeting to form Y-shaped arches. Distal region of caudal series sharply decurved. Lateral zygapophysial faces united to form single anterior and posterior facets. Scapula narrow distally. Pelvic elements much reduced. Epipodial elements short, rarely separated by a cleft. Phalangeal elements short, with angulated or rounded margins. Maxillary relatively short compared with the premaxillary. Orbits very large. Postorbital bar narrow. Teeth numerous, isodont, situated in open grooves.

Several of the Triassic ichthyosaurian forms which are represented by fragmentary material seem to stand nearer to *Ichthyosaurus* than to any of the typical Triassic genera, and may be referred tentatively to that genus. It is not improbable that some of these when represented by better material may be shown to be generically distinct from *Ichthyosaurus*. On the other hand it is to be presumed that *Ichthyosaurus* was in existence in late Triassic time, and there appears to be no reason why it should not be represented in the formations of that period in Europe where it was so abundant in the early Jurassic.

ICHTHYOSAURUS CARINATUS Sauvage.

Ichthyosaurus carinatus Sauvage, Ann. Sc. Geol., t. 7, art. 6, 1876.

From the Rhaetic of the vicinity of Autun, France.

According to Sauvage this species is large, and is characterized by the flattening of the centrum and the carina of the inferior face of the centrum in the middle dorsal region. The anterior dorsal centra are oval; the articular faces are deeply concave; the diapophyses and parapophyses are widely separated.

MEASUREMENTS OF AN ANTERIOR DORSAL CENTRUM.

Anteroposterior diameter of centrum	60 mm.
Height of centrum	160
Width of centrum	145

Length, 100; height, 266; width, 242.

MEASUREMENTS OF A MIDDLE DORSAL CENTRUM.

Anteroposterior diameter of centrum	57 mm.
Height of centrum	168
Width of centrum	173

Length, 100; height, 295; width, 303.

The specimens figured by Sauvage (1883, pl. 8) seem to represent a form which is generically closely allied if not identical with *Ichthyosaurus*.

ICHTHYOSAURUS(?) RHETICUS Sauvage.

Ichthyosaurus rheticus Sauvage, Ann. Sc. Geol., t. 7, art. 6.

Rachitrema pellati Sauvage, Ann. Sc. Geol., t. 14, art. 3, p. 5; and Bull. Soc. D'Hist. Nat. D'Autun, t. 16, p. 315.

From the Rhaetic of the vicinity of Autun, France.

This is a large species in which the centra of the dorsal vertebra are much higher than long (anteroposterior diameter or length, 100; height, 234; width, 243). The centra are strongly biconcave, the concavity commencing at the margin. There is no ridge on the inferior face of the centra. The diapophyses and parapophyses are large and are nearly in contact on the specimens described.

Of this species there was originally described a small amount of material representing vertebrae, ribs, a portion of a scapula, and a femur. Other material originally described under the name *Rachitrema pellati* has recently been referred by Sauvage (1903) to *I.*(?) *rheticus.* Von Huene (1902, p. 71) has suggested that *Rachitrema* is an ichthyosaurian rather than a dinosaur.

The material which has been referred to *I.*(?) *rheticus* and to *Rachitrema pellati* by Sauvage, and was figured by him (1883), appears to represent an ichthyosaurian having its closest affinities with the Ichthyosaurinae. The vertebra of *I.*(?) *rheticus* figured by Sauvage (1883, pl. 8, fig. 4*a*) evidently represents a middle dorsal in which the diapophyses are almost in contact with the large parapophyses (fig. 154). In no representative of the shastasaurine group are parapophyses known behind the region in which the diapophysial articular faces become separated from the neurapophysial faces. The upper arch referred to *Rachitrema pellati* is however somewhat more primitive in its characters than the corresponding arches of the Jurassic ichthyosaurs.

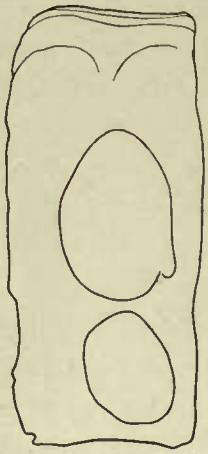
Fig. 154. *Ichthyosaurus*(?) *rheticus.* Sauvage. Outline, side view, of middle dorsal vertebral centrum, slightly reduced. (Adapted from Sauvage.)

ICHTHYOSAURUS(?) HECTORI Lydekker.

Ichthyosaurus australis Hector, Trans. New Zealand Inst., vol. 6, p. 355.

Ichthyosaurus hectori Lydekker, Catlg. Foss. Rept. Brit. Mus., pt. 2, p. 113.

In the collections of fossil reptilia of New Zealand examined by Hector, the genus *Ichthyosaurus* was represented by a single vertebral centrum, in a micaceous sandstone from the rocks of Mount Potts, in the Rangitata district of the province of Canterbury. The beds were said to be identical with strata that in other parts of the colony were considered to be Triassic.

The name *I. australis,* which Hector first used for this form, having been used for a Cretaceous species from Australia, Lydekker named the species after Hector.

So little is known of this form that no suggestion regarding its affinities can be made.

ICHTHYOSAURUS, sp.

To this genus there have been referred a number of ichthyosaurian remains obtained in Rhaetic beds at Aust Cliff near Bristol, England. This material was referred to *Ichthyosaurus* by Phillips (1871). Lydekker (1889) suggested the resemblance of a tooth from this locality to the type of *I. lonchiodon.* Von Huene (1902) mentions numerous vertebrae, and a large snout fragment of the size of *I. platyodon* and *trigonodon* from the beds at Aust Cliff.

Date of issue:
September 30, 1908.

ERRATA.

Page 7. Baur's Article 2, 1887, appears to antedate Article 1. See also p. 10, paragraph 4; p. 76, paragraph 2, line 7; p. 82, paragraph 5; p. 94, *Mixosaurus* literature, Baur; p. 95, *M. cornalianus*, Baur reference; p. 99, paragraph 4.

Page 23. Paragraph 3, line 12, for "about 38," read "over 80."

Page 93. Paragraph 5, line 1, after fourth word insert "the."

PLATE 1.

ERRATA.

Page 7. Baur's Article 2, 1887, appears to antedate Article 1. See also p. 10, paragraph 4; p. 76, paragraph 2, line 7; p. 82, paragraph 5; p. 94, *Mixosaurus* literature, Baur; p. 95, *M. cornalianus*, Baur reference; p. 99, paragraph 4.

Page 23. Paragraph 3, line 12, for "about 38," read "over 80."

Page 93. Paragraph 5, line 1, after fourth word insert "the."

Page 7. Fraas, 1891, for "Suddeutchen" read "Süddeutschen; for "and" read und; Fraas, 1896, for "Schwabische" read Schwäbische.
Page 8. For "Myer" read Meyer. Under Yakowlew, 1902 (2) for "Triassichen" read Triassische.
Page 10. Paragraph 2, line 1, for "1873" read 1876; line 3, for "1876" read 1883; paragraph 4, line 2, for "1877" read 1887.
Page 13. Line 1, for "Rhordorf" read Rohrdorf.
Page 14. Paragraph 2, line 3, for *"rhaeticus"* read *rheticus.*
Page 17. Last line of footnote, after "Publ," read Geol.
Page 19. Last line of text, for "cephalapods" read cephalopods.
Page 26. Legend of figure 8, for *"Merriami"* read *Merriamia.*
Page 29. Paragraph 3, line 10, for "vertebrate" read vertebrae.
Page 32. Paragraph 1, line 7, for "fig. 134" read fig. 136.
Page 34. Legend of figure 33, for *"atispinus"* read *altispinus.*
Page 80. Paragraph 1, last line, and third footnote, for "Jackel" read Jaekel.
Page 90. *Mixosaurus* (?) *atavus* literature, line 3, for "Südeutschen" read Süddeutschen; line 4, for "and" read und.
Page 103. *Cymbospondylus* literature, line 3, after "Publ." read Geol.
Page 104. *Cymbospondylus petrinus* literature, line 3, after "Publ." read Geol.
Page 123. *Cymbospondylus piscosus* literature, line 2, after "Publ." read Geol.

PLATE 1.

EXPLANATION OF PLATE 1.

Fig. 1. Exposure of Middle Triassic limestones on the south fork of American Cañon, West Humboldt Range, Nevada. Limestones extending from Saurian Hill (*S*) to the end of the ridge beyond Fossil Hill (*F*).

Fig. 2. Exposures of Upper Triassic, Hosselkus Limestone, on Brock Mountain, Shasta County, California. The massive upper limestones are conspicuously pinnacled. The more shaly beds of the lower horizon are less conspicuous, and are largely covered with thick brush.

Fig. 3. Detail from fig. 2 showing the contorted shaly limestones of the lower horizon from their upper contact down almost to the Pit Shale.

Fig. 1.—Middle Triassic limestones, West Humboldt Range, Nevada. *S*, Saurian Hill; *F*, Fossil Hill.

Fig. 2.—Upper Triassic, Shasta County, California. Upper and lower horizons.

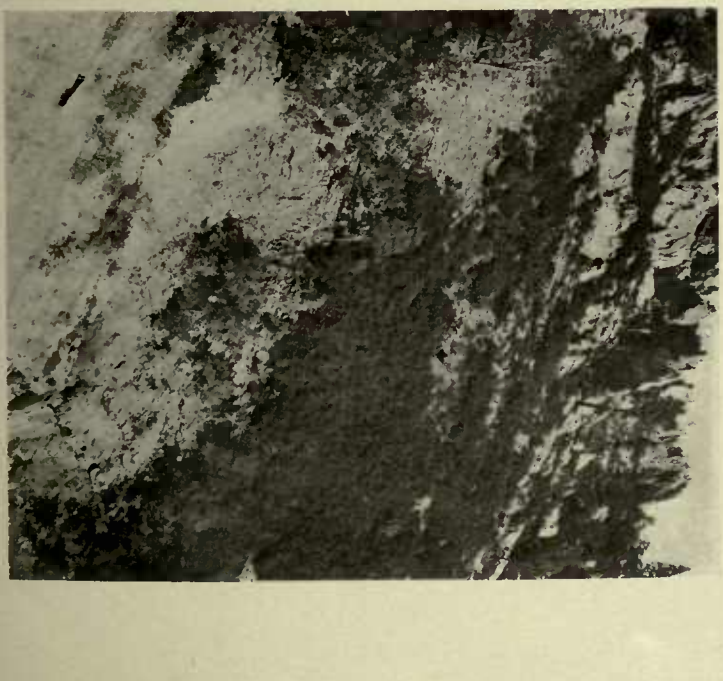

Fig. 3.—Upper Triassic, mainly lower beds, Shasta Co., Calif.

PLATE 2.

EXPLANATION OF PLATE 2.

Cymbospondylus petrinus Leidy.

Lateral view of skull, no. 9950, × ⅕.

From the Middle Triassic of West Humboldt Range, Nevada.

LEGEND.

Pm, premaxillary.
M, maxillary.
N, nasal.
L, lachrymal.
F, frontal.
Pn, pineal foramen.
Pr, parietal.
Pf, prefrontal and postfrontal.
Pto, postorbital.
J, jugal.
Or, orbit.
Sq, squamosal.
St, supratemporal.
Q, quadrate.
Qj, quadratojugal.
Ar, articular.
Sa, surangular.
An, angular.
D, dentary.
Sp, splenial.


D
Pm
Sp
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N
L
F
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Pf
Pr
Or
Pto
J
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Sq
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Qj
Q
Ar
An

PLATE 3.

EXPLANATION OF PLATE 3.

Cymbospondylus petrinus Leidy.
Superior view of skull, no. 9950, × ⅕.
From the Middle Triassic of West Humboldt Range, Nevada.

LEGEND.

Pm, premaxillary.
M, maxillary.
N, nasal.
L, lachrymal.
Or, orbit.
F, frontal.
Pn, pineal foramen.
Pr, parietal.
Pf, prefrontal and postfrontal.
Pto, postorbital.
J, jugal.
Sq, squamosal.
St, supratemporal.
Qj, quadratojugal.
Q.f., quadrate foramen.
Q, quadrate.
So, supraoccipital.
Bo, basioccipital.
Pt, pterygoid.
Ar, articular.
Sa, surangular.
An, angular.
Cn, coronoid.
Pt, pterygoid.


Pm
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Q.j.
Cn
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Ar
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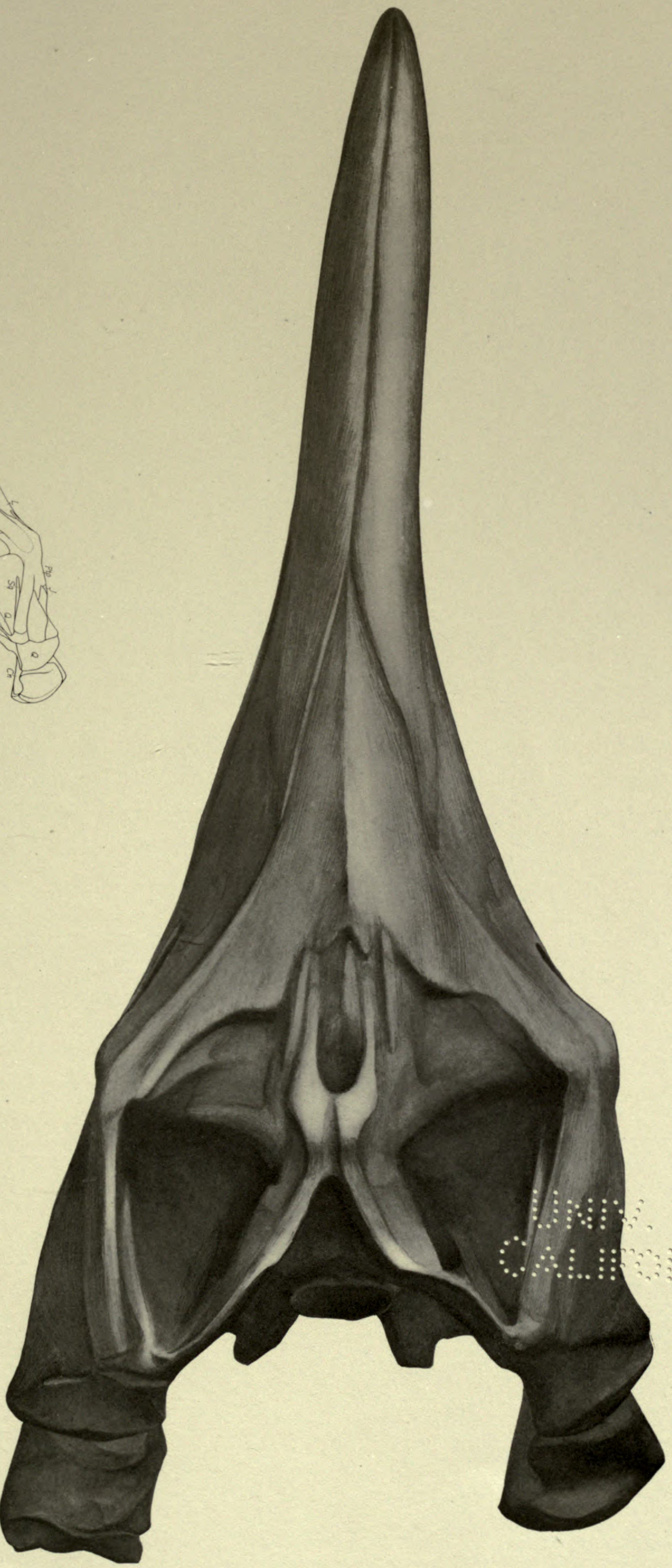


PLATE 4.

EXPLANATION OF PLATE 4.

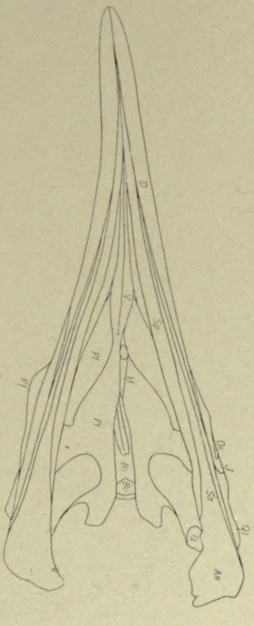
Cymbospondylus petrinus Leidy.

Inferior view of skull, no. 9950, $\times \frac{1}{5}$.

From the Middle Triassic of West Humboldt Range, Nevada.

LEGEND.

D, dentary.
Sp, splenial.
Sa, surangular.
A, angular.
V, prevomer?
Pl, palatine.
Pt, pterygoid.
X, ectopterygoid?
H, hyoid.
Bs, basisphenoid.
Bo, basioccipital.
Q, quadrate.
Qj, quadratojugal.
J, jugal.
Or, orbit.
Pf, prefrontal and postfrontal.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V
Sp
Pl
Pl
H
Pt
Os
J
Sa
Bs
Bo
Qj
Q
An

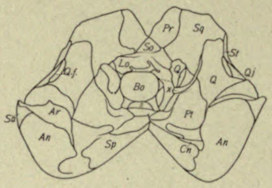
PLATE 5.

EXPLANATION OF PLATE 5.

Cymbospondylus petrinus Leidy.

From the Middle Triassic of West Humboldt Range, Nevada.

Fig. 1. Posterior view of skull, no. 9950, × ⅕.



Legend for guide figure.

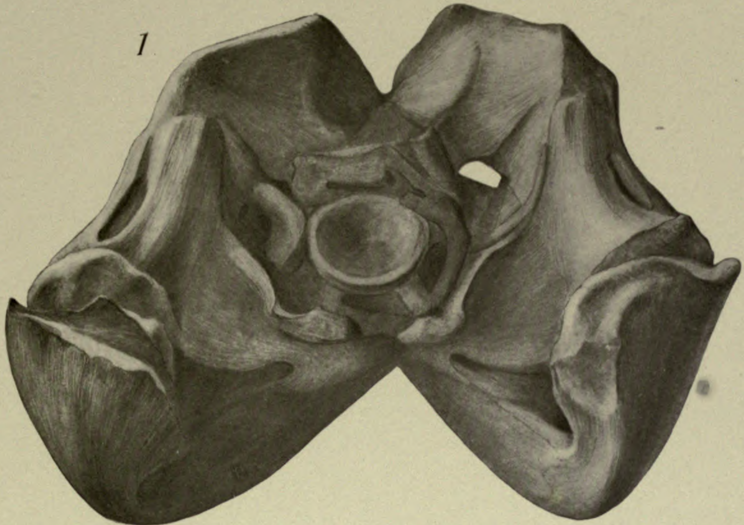
Pr, parietal.
Sq, squamosal.
St, supratemporal.
Qj, quadratojugal.
Q, quadrate.
Q.f., quadrate foramen.
So, supraoccipital.
Lo, lateral occipital (?).
Bo, basioccipital.
S, basisphenoid.
Pt, pterygoid.
X, indeterminate (stapes?).
Ar, articular.
Sa, surangular.
An, angular.
Sp, splenial.
Cn, coronoid.

Fig. 2. Orbital region showing complete sclerotic ring, no. 9954, × ⅓.

Fig. 3. Inner side of posterior end of left ramus of the mandible, no. 9913, × ⅓. *A,* articular; *Cn,* coronoid; *An,* angular; *H,* hyoid; *Q,* quadrate.

Fig. 4. Superior view of right articular, no. 9913, × ⅓.

1



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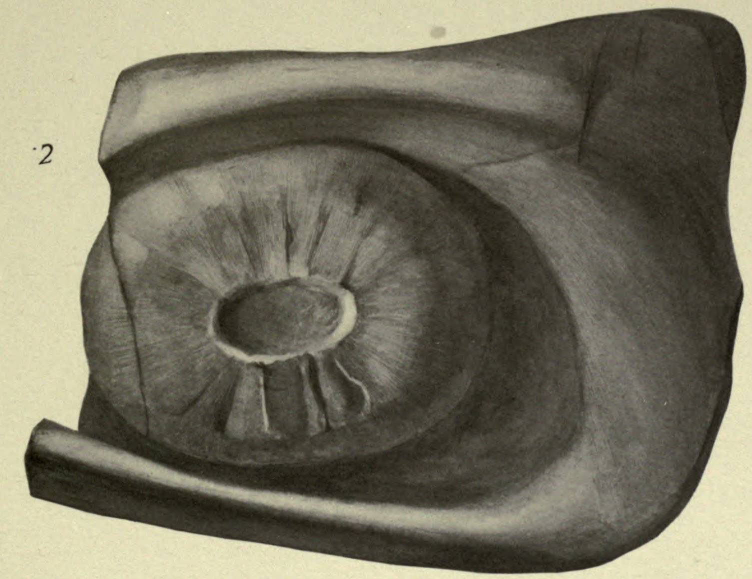

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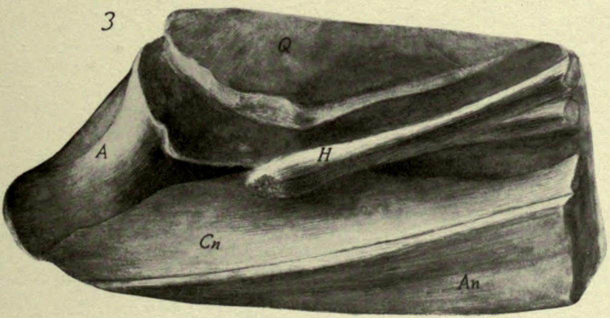

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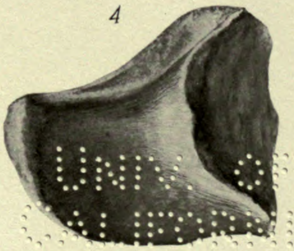


PLATE 6.

EXPLANATION OF PLATE 6.

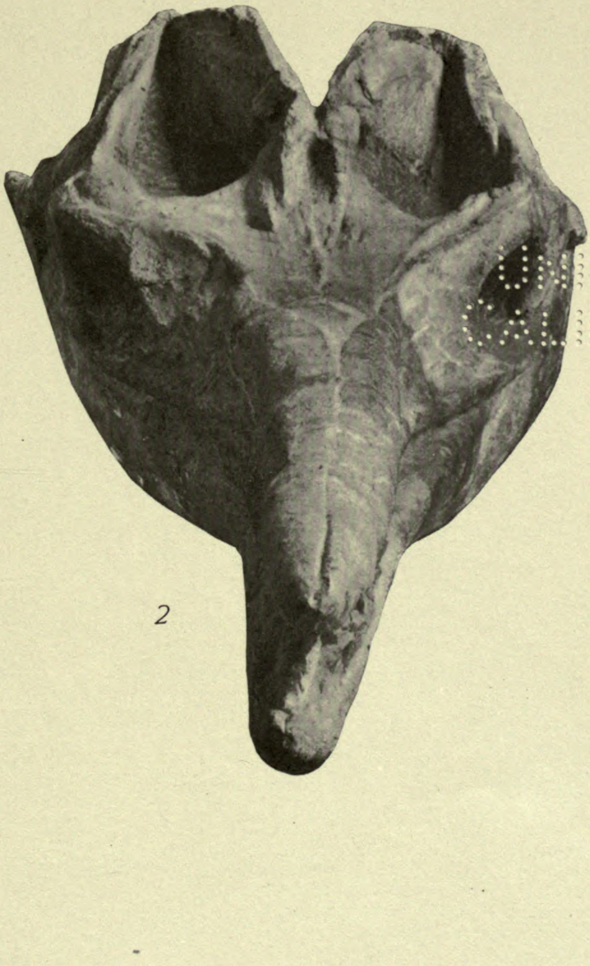
Cymbospondylus petrinus Leidy.

From the Middle Triassic of West Humboldt Range, Nevada.

Fig. 1. Lateral view of cranium, no. 9913, about $^{15}/_{100}$ of natural size.

Fig. 2. Anterior view of cranium, no. 9950, a little less than $1/5$ of natural size.

1



2

PLATE 7.

EXPLANATION OF PLATE 7.

Fig. 1. *Cymbospondylus petrinus* Leidy. Photograph of mounted specimen, no. 9950, about 1/16 of natural size. Restoration is limited to the distal portion of some of the ribs. From the Middle Triassic of West Humboldt Range, Nevada.

Fig. 2. *Delphinosaurus perrini* Merriam. Type specimen, no. 9119, a little less than 1/8 of natural size. From the Upper Triassic of Shasta County, California.

Fig. 3. *Delphinosaurus perrini* Merriam. Specimen 10998. About 1/10 of natural size. From the Upper Triassic of Shasta County, California.

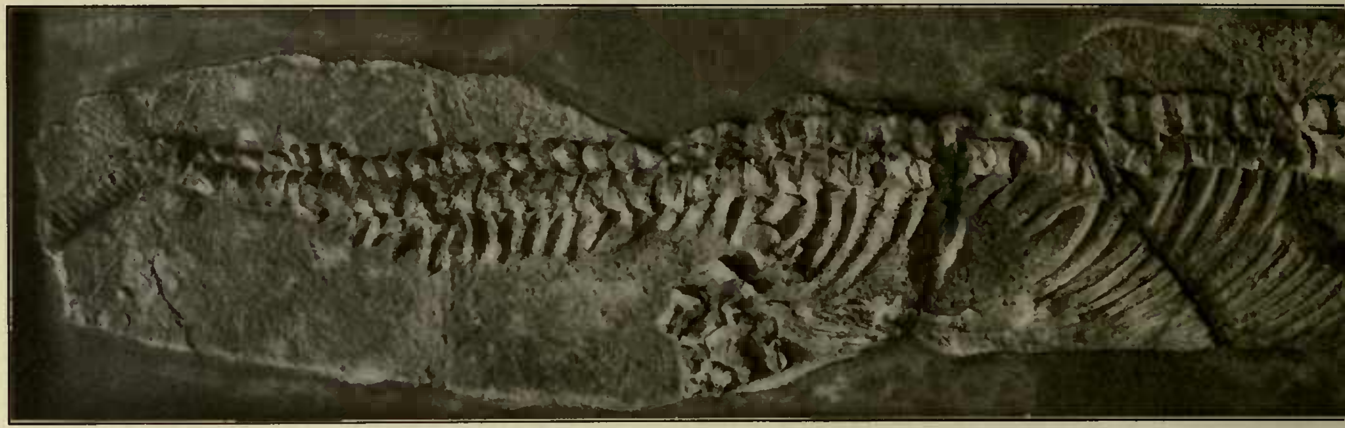


Fig. 2.—*DELPHINOSAURUS PERRINI* Merriam.

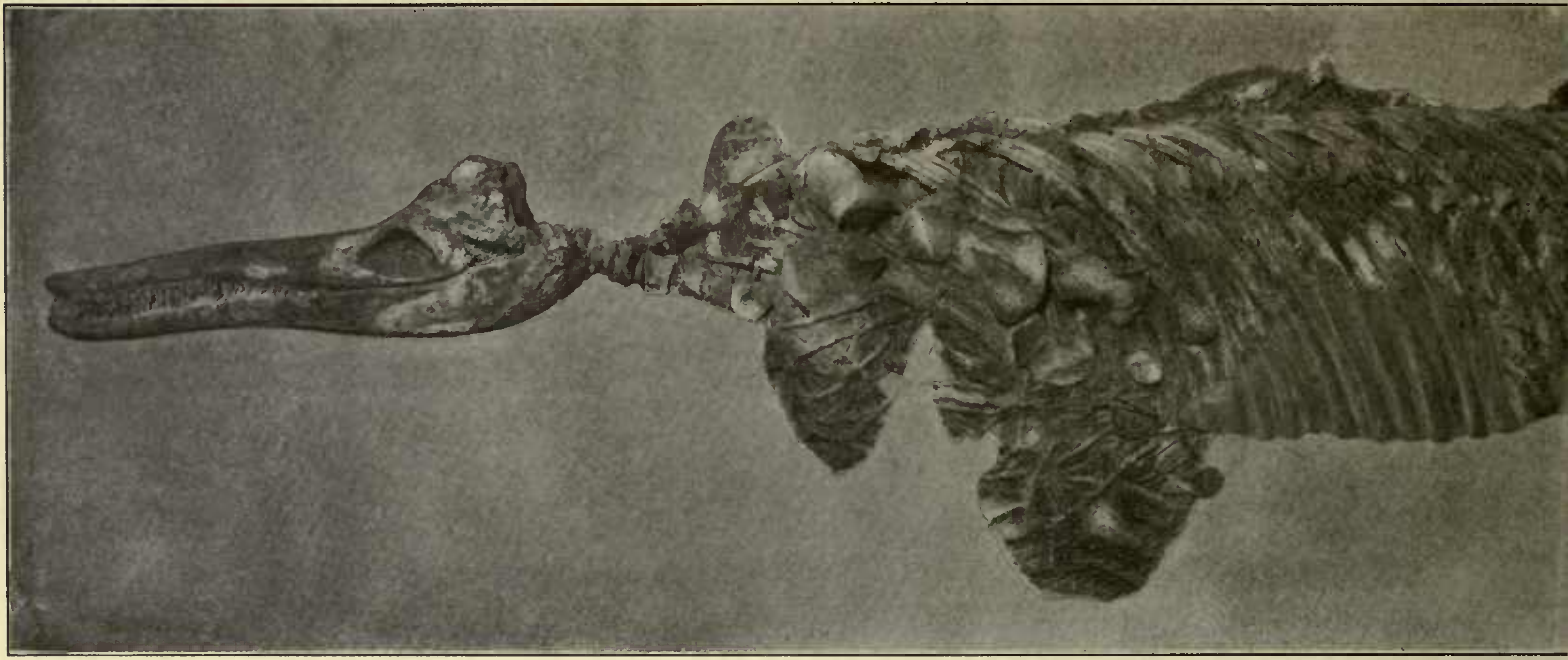
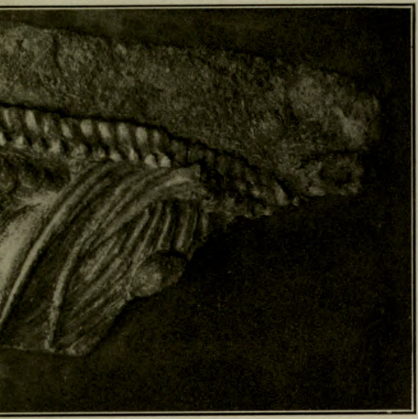
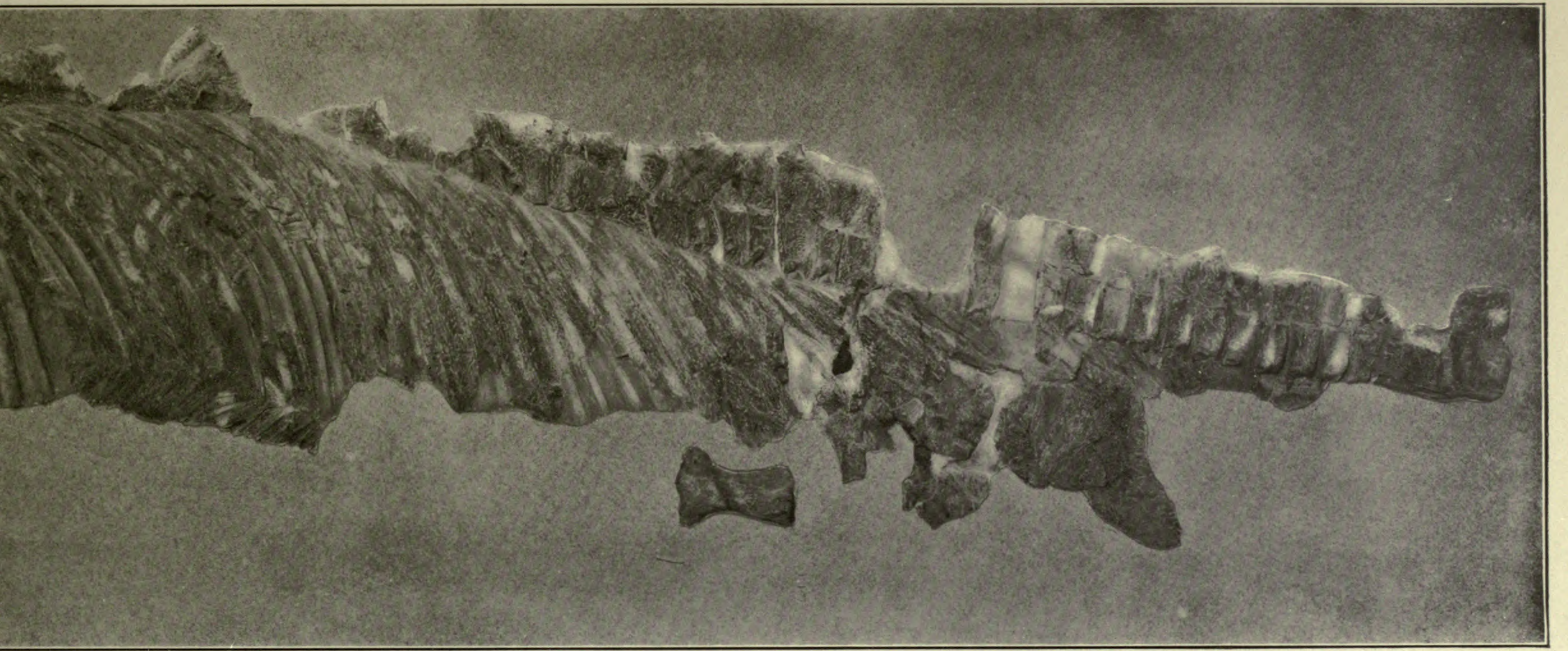


Fig. 1.—*CYMBOSPON*





US PETRINUS Leidy.

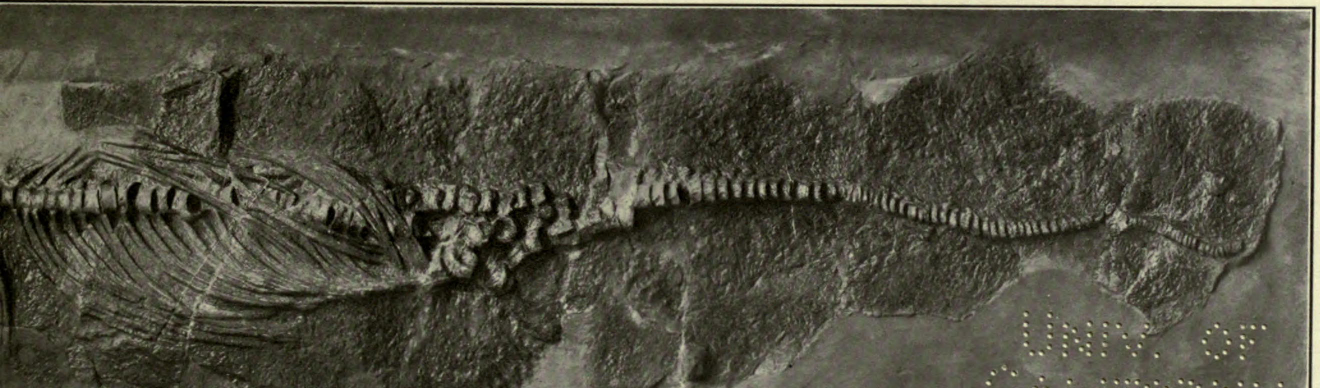


FIG. 3.—*DELPHINOSAURUS PERRINI* Merriam.

PLATE 8.

EXPLANATION OF PLATE 8.

Cymbospondylus petrinus Leidy.

From the Middle Triassic of West Humboldt Range, Nevada.

All figures four-ninths of natural size.

Fig. 1*a*-1*d*. Atlas and axis, no. 9943.
  1*a*, axis, inferior view, anterior face to right.
  1*b*, atlas, anterior view.
  1*c*, atlas, superior view, anterior face to right.
  1*d*, atlas, lateral view, anterior face to left.

Fig. 2. Atlas and axis, no. 9154, superior view.

Fig. 3. Atlas and axis, no. 9913, inferior view.

Fig. 4. Upper arch of cervical vertebra, no. 9943, anterior view.

Fig. 5. Atlas, lateral view, no. 9913, anterior face to right.

Fig. 6. Axis, lateral view, no. 9950.

Fig. 7*a*-7*c*. Third cervical, no. 9950.
  7*a*, lateral view; 7*b*, anterior view; 7*c*, upper arch.

Fig. 8. Fifth cervical, no. 9950.

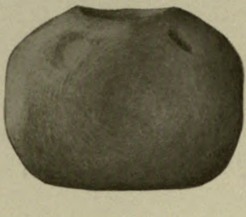
Fig. 9. Sixth cervical, no. 9950.

Fig. 10. Anterior dorsal, no. 9950.

Fig. 11. Middle dorsal, no. 9154.

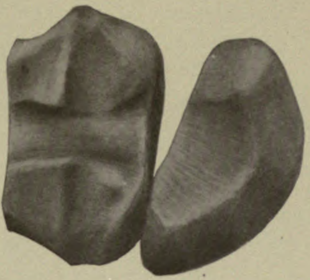
Fig. 12. Middle dorsal, no. 8128.


1a


1b


1c


1d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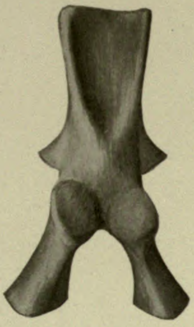
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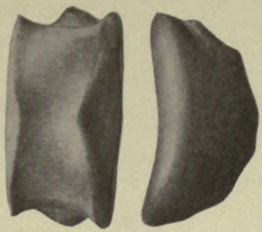
7c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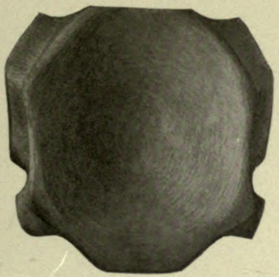
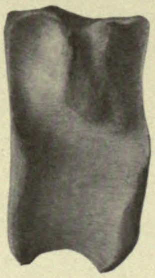

7b


7a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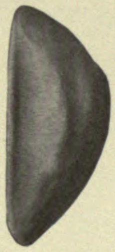
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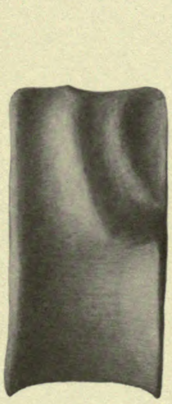
12


11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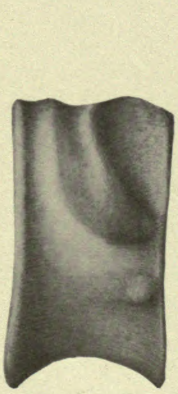
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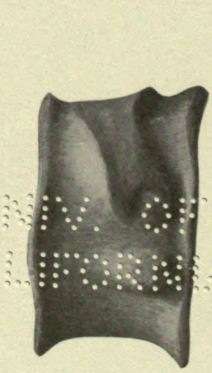
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PLATE 9.

EXPLANATION OF PLATE 9.

Cymbospondylus petrinus Leidy.

From the Middle Triassic of West Humboldt Range, Nevada.

All figures four-ninths of natural size.

Fig. 1. Posterior dorsal vertebra, no. 9950.

Fig. 2. Posterior dorsal vertebra, no. 8128.

Fig. *3a* and *3b*. Posterior dorsal vertebra, no. 8128, situated somewhat farther back in the series than the centrum represented by fig. 2.

3a, anterior view; *3b,* lateral view.

Fig. 4. Anterior caudal vertebra, no. 9947.

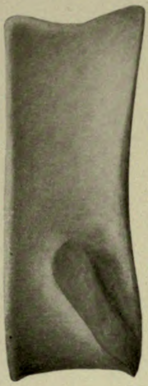
Fig. 5. Middle caudal vertebra, anterior to bend of tail, no. 9947.

Fig. 6. Middle caudal vertebra, situated at the anterior end of caudal flexure, no. 9947.

Fig. 7. Posterior caudal vertebra, situated at about the middle of the caudal flexure, no. 9947.

Fig. *8a* and *8b*. Posterior caudal vertebra, situated near the posterior end of the tail, no. 9947.

8a, lateral view, with chevron; *8b,* anterior view.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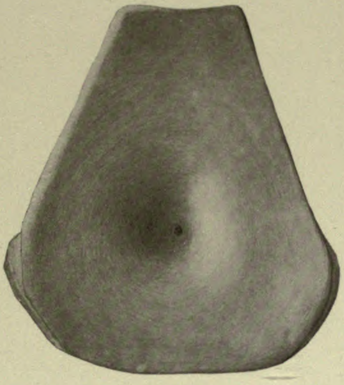
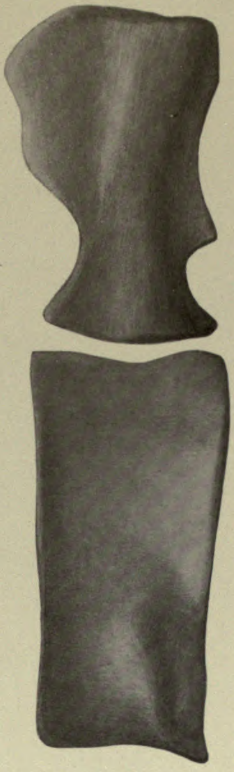

3a


2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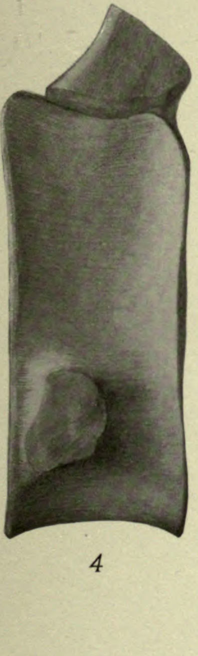
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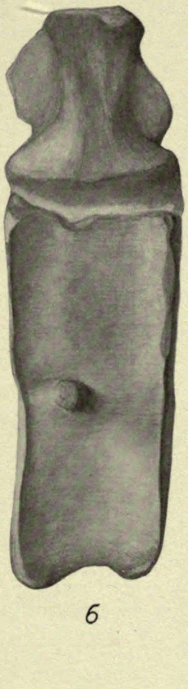
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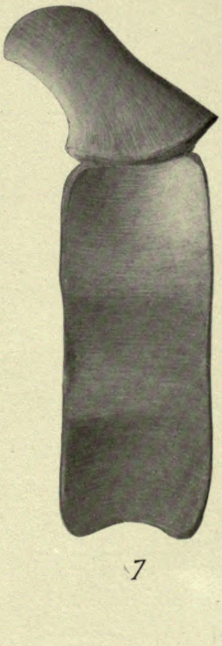
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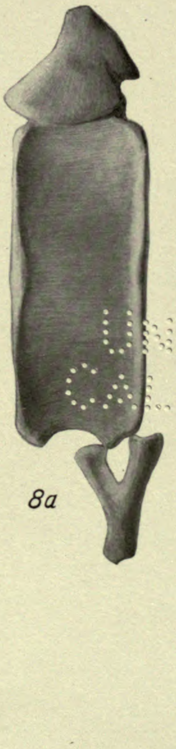

8a

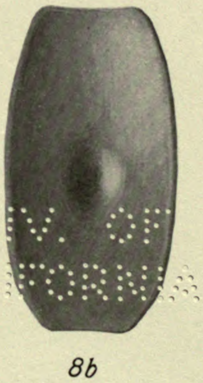

8b

PLATE 10.

EXPLANATION OF PLATE 10.

All specimens from the Middle Triassic of West Humboldt Range, Nevada.

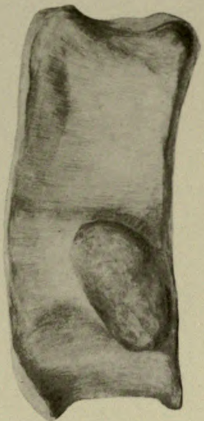
Fig. 1. *Cymbospondylus*(?) *natans*, n. sp. Vertebrae from middle region of caudal fin, no. 10624, × 1/2.

Figs. 2*a* and 2*b*. *Cymbospondylus petrinus* Leidy, anterior caudal centrum, no. 8120, × 2/3. 2*a*, lateral view. 2*b*, inferior view.

Figs. 3-7. *Cymbospondylus petrinus* Leidy. Ribs, no. 9950, × 4/9.

3. Anterior cervical rib.
4. Posterior cervical rib.
5. Anterior dorsal rib.
6. Middle dorsal rib.
7. Caudal rib.

Fig. 8. *Cymbospondylus petrinus* Leidy. Abdominal ribs, no. 9154, about 1/4 of natural size.



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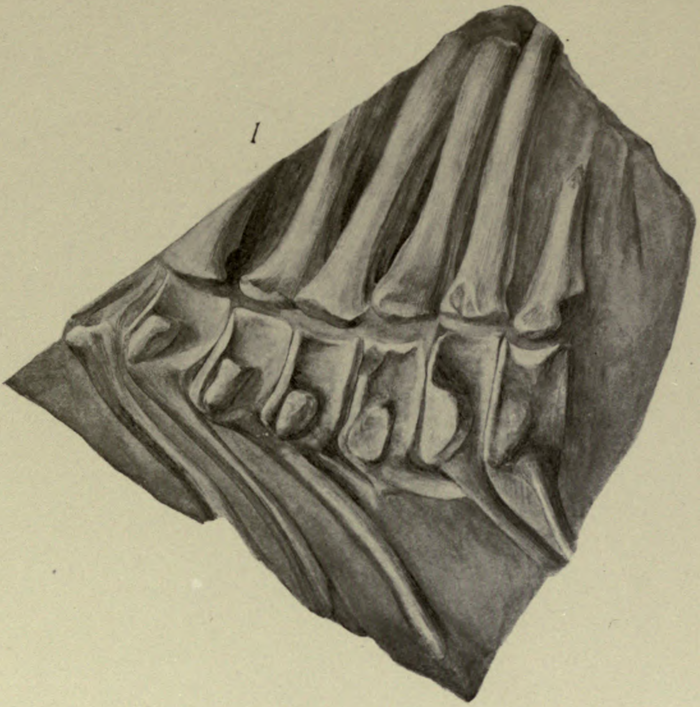

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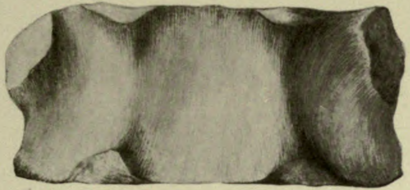

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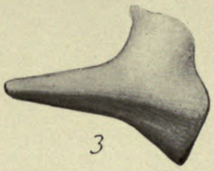

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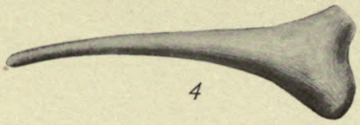

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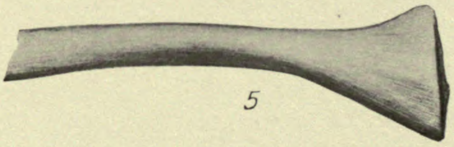

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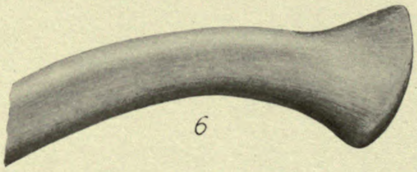

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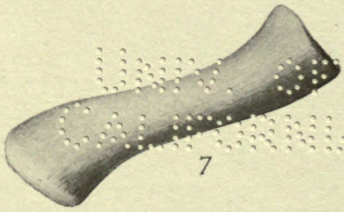

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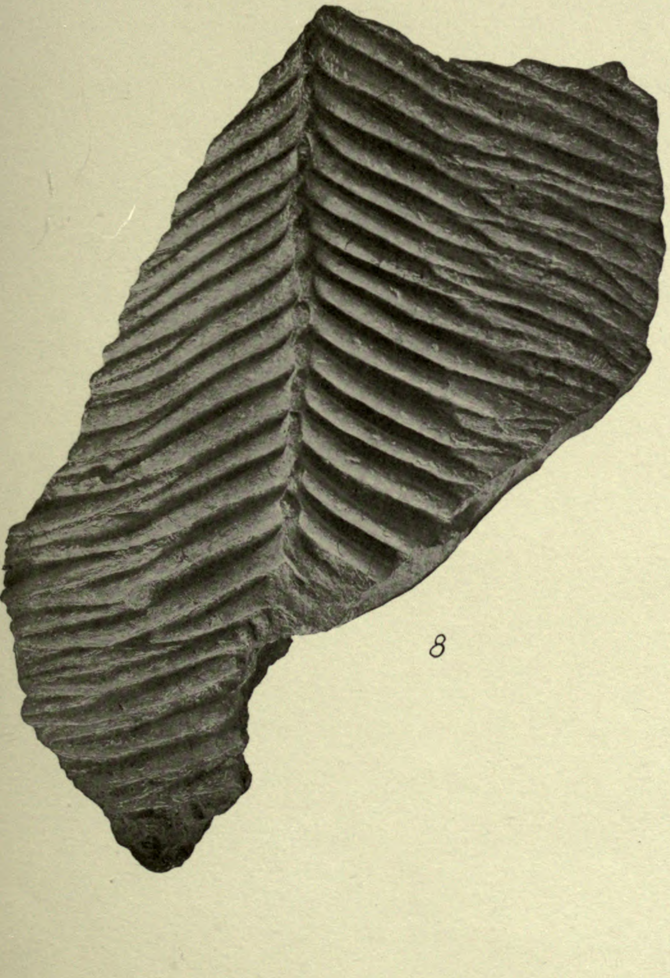

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PLATE 11.

EXPLANATION OF PLATE 11.

Cymbospondylus petrinus Leidy.

Anterior limb and arch, × 2/9.

From the Middle Triassic of West Humboldt Range, Nevada.

Fig. 1. No. 9154. *Cl,* right clavicle.

Fig. 2. No. 9950. Left side: *Sc,* scapula; *Co,* coracoid; *H,* humerus; *R,* radius; *U,* ulna; *Car,* carpals.

1

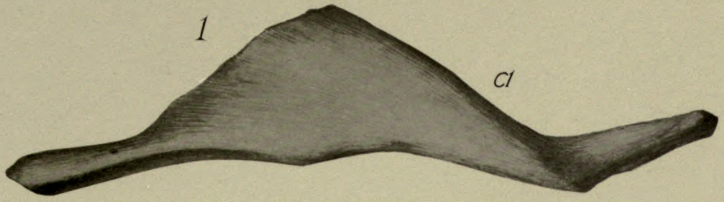

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PLATE 12.

EXPLANATION OF PLATE 12.

Cymbospondylus petrinus Leidy.

Posterior limb and arch elements, no. 9947. From the Middle Triassic of West Humboldt Range, Nevada.

All figures one-third of natural size.

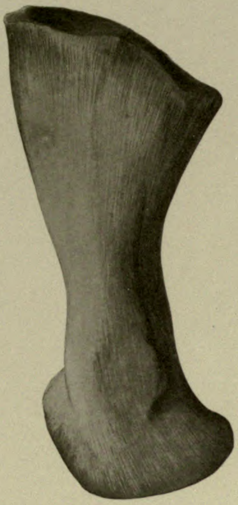
Fig. 1. Right ? ilium, posterior side.

Fig. 2. Left ? pubis, superior side.

Fig. 3. Left ? ischium, superior side.

Fig. 4. Right ? ilium, inner side.

Fig. 5. Left ? posterior limb. *F,* femur; *T,* tibia; *Fb,* fibula; *Trs,* tarsals.



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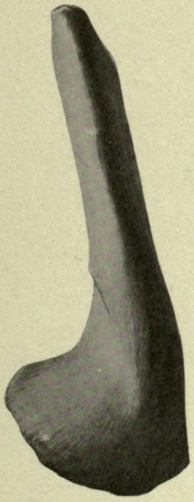

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5

PLATE 13.

EXPLANATION OF PLATE 13.

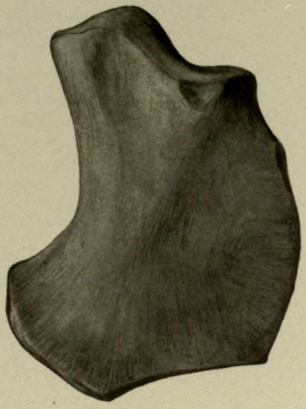
Figs. 1*a* and 1*b*. *Cymbospondylus*(?) *natans,* n. sp. Right humerus. no. 9873, × 1. From the Middle Triassic, West Humboldt Range, Nevada.

1*a,* superior side; 1*b,* inferior side.

Fig. 2. *Cymbospondylus nevadanus,* n. sp. Tibia? no. 10620, × 4/9. From the Middle Triassic, New Pass Range, Nevada.

Fig. 3. *Cymbospondylus nevadanus,* n. sp. Fibula?, no. 10620, × 4/9. From the Middle Triassic, New Pass Range, Nevada.

Figs. 4*a* and 4*b*. *Cymbospondylus nevadanus,* n. sp. Two views of a caudal rib, no. 10620, × 4/9. From the Middle Triassic, New Pass Range, Nevada.



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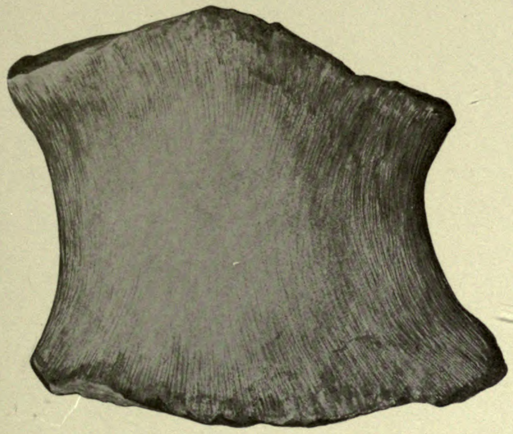
1b



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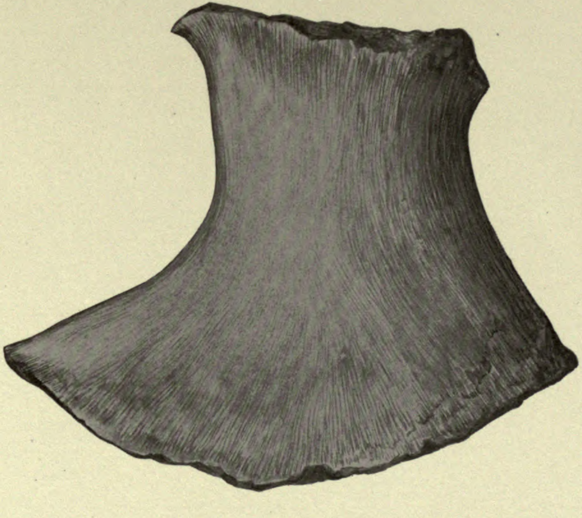

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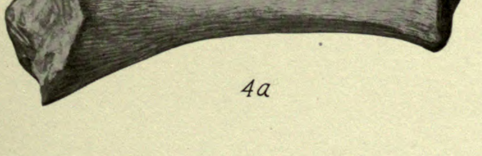

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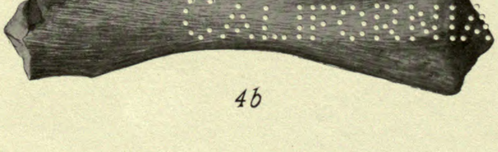


4b

PLATE 14.

EXPLANATION OF PLATE 14.

All specimens from the Upper Triassic of Shasta County, California.

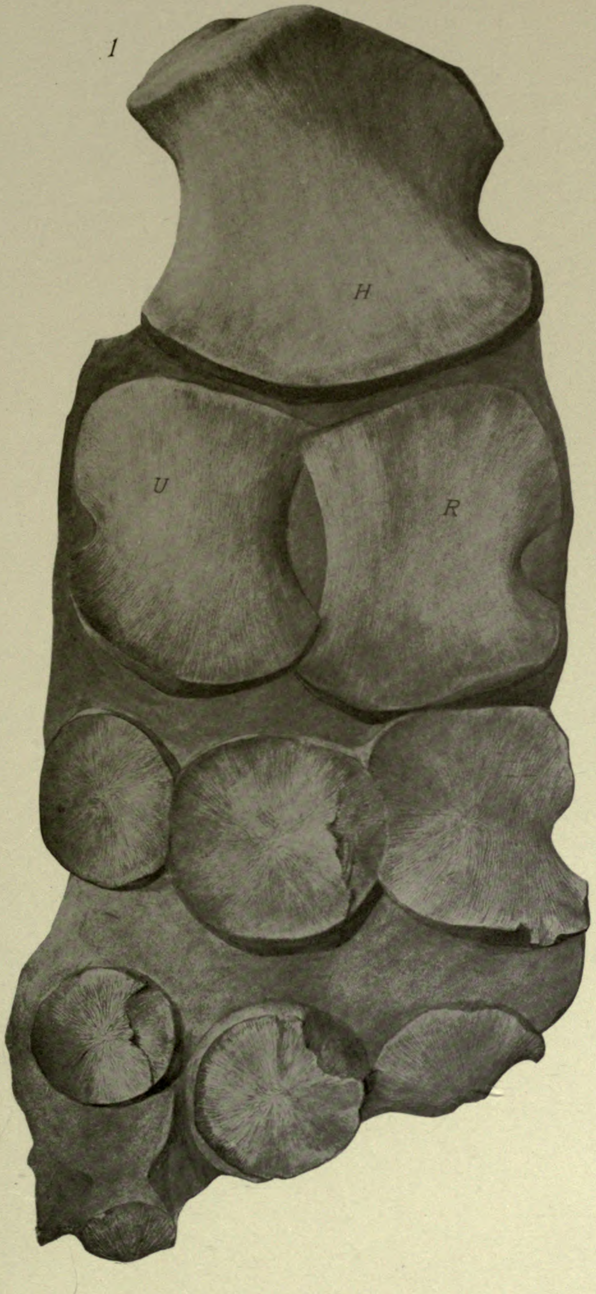
Fig. 1. *Delphinosaurus perrini* Merriam. Right anterior limb, no. 9082, × ¾. *H,* humerus; *R,* radius; *U,* ulna.

Fig. 2. *Delphinosaurus perrini* Merriam. Left? scapula, no. 9082, × ¾.

Fig. 3. *Delphinosaurus perrini* Merriam. Right coracoid, no. 9082, × ¾.

Fig. 4. *Toretocnemus californicus* Merriam. Anterior caudal vertebrae, no. 8100. Natural size.

1



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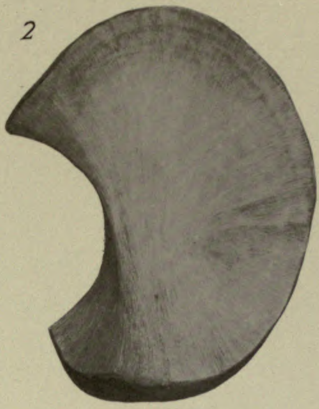

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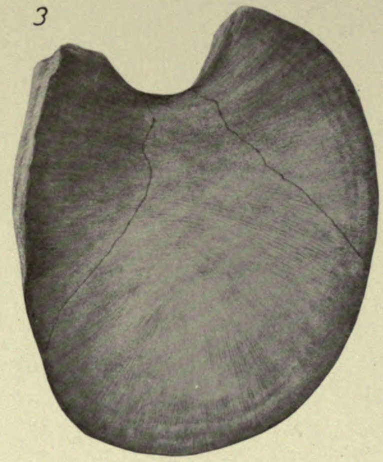

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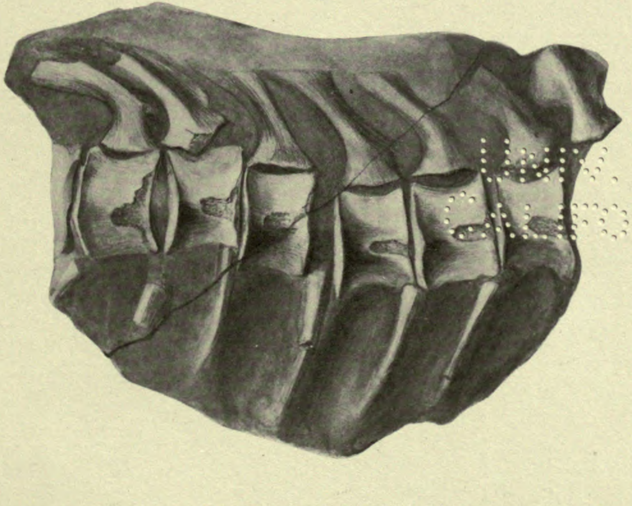


PLATE 15.

EXPLANATION OF PLATE 15.

All specimens from the Upper Triassic of Shasta County, California.

Figs. 1*a*-1*b*. *Shastasaurus osmonti* Merriam. no. 9076, × ⅓. Anterior distal angle of humerus, posterior distal angle of ulna, and posterior side of radiale, restored from elements of right limb of this specimen.

1*a*. Superior side of left anterior limb.

H, humerus; *R,* radius; *U,* ulna; *Rl,* radiale.

1*b*. Proximal end of humerus shown in fig. 1*a*.

Figs. 2*a* and 2*b*. *Shastasaurus careyi* (?) Merriam. no. 9614, × ⅓.

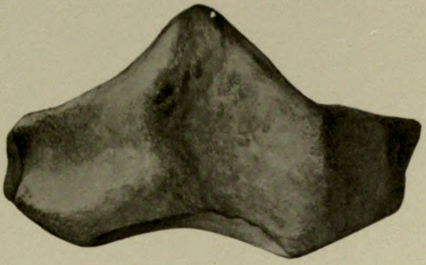
2*a*. Superior side of right anterior limb.

H, humerus; *R,* radius.

2*b*. Proximal end of humerus shown in fig. 2*a*.

Fig. 3. *Shastasaurus osmonti* Merriam. Marginal view of carpal or phalangeal element, no. 9081, × ⅓.

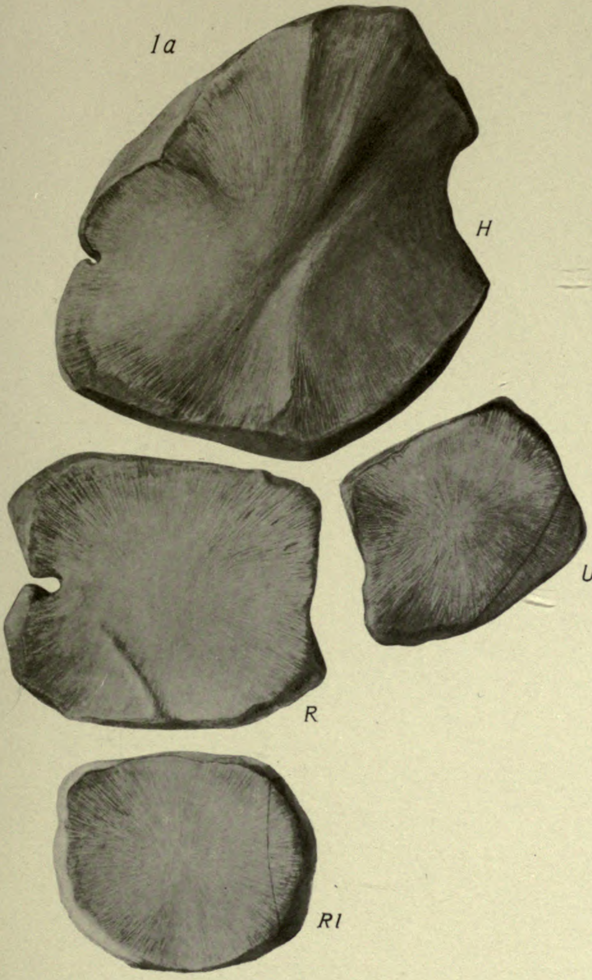
Fig. 4. *Shastasaurus osmonti* Merriam. Elements of a transverse row of ossicles in the mesopodial or metapodial region of the anterior limb, showing reduction of the posterior element, no. 9081, × ⅓.



1b

2b

1a



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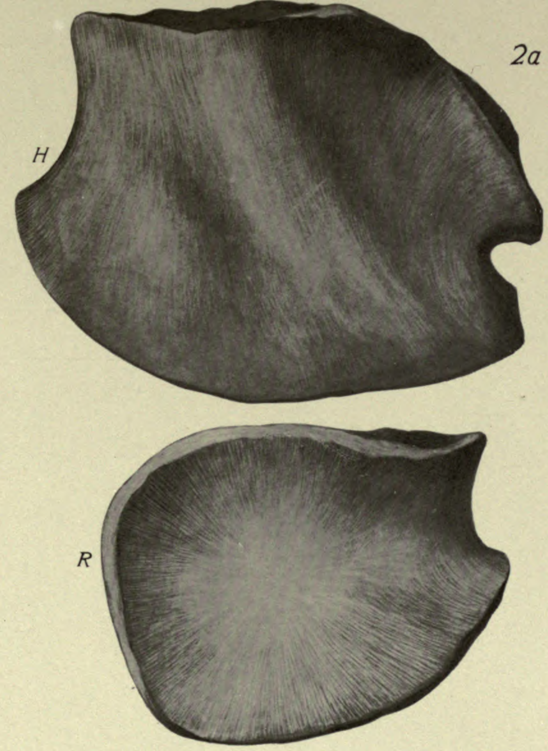

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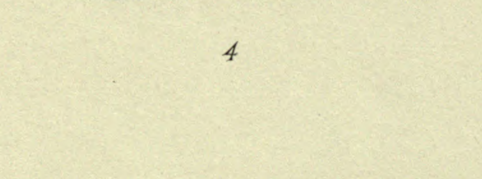

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PLATE 16.

EXPLANATION OF PLATE 16.

Shastasaurus osmonti Merriam.

From the Upper Triassic of Shasta County, California.

All figures one-third of natural size.

Fig. 1. Superior side of right coracoid, no. 9076.

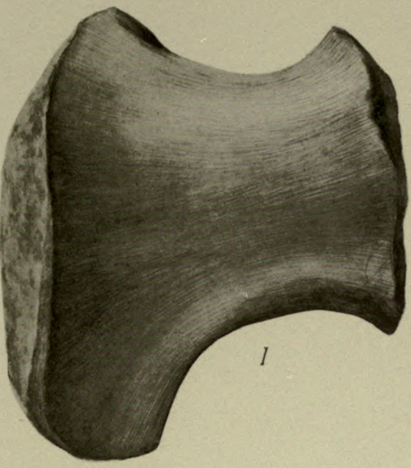
Fig. 2. Superior or inner side of right scapula, no. 9076.

Fig. 3. Ischium, no. 9608.

Fig. 4. Ilium, no. 9608.

Fig. 5. Pubis, no. 9608.

Fig. 6. Posterior limb, no. 9608.
F, femur; *T,* tibia; *Fb,* fibula; *Trs,* tarsals.



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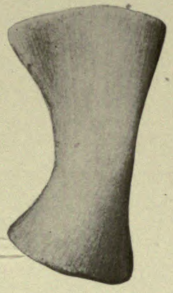

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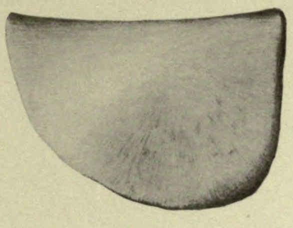

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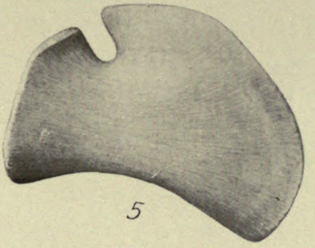

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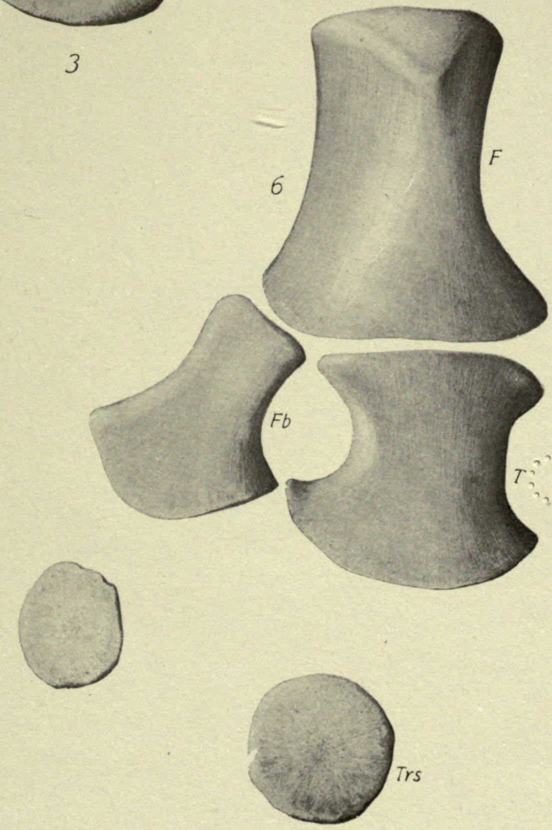


6

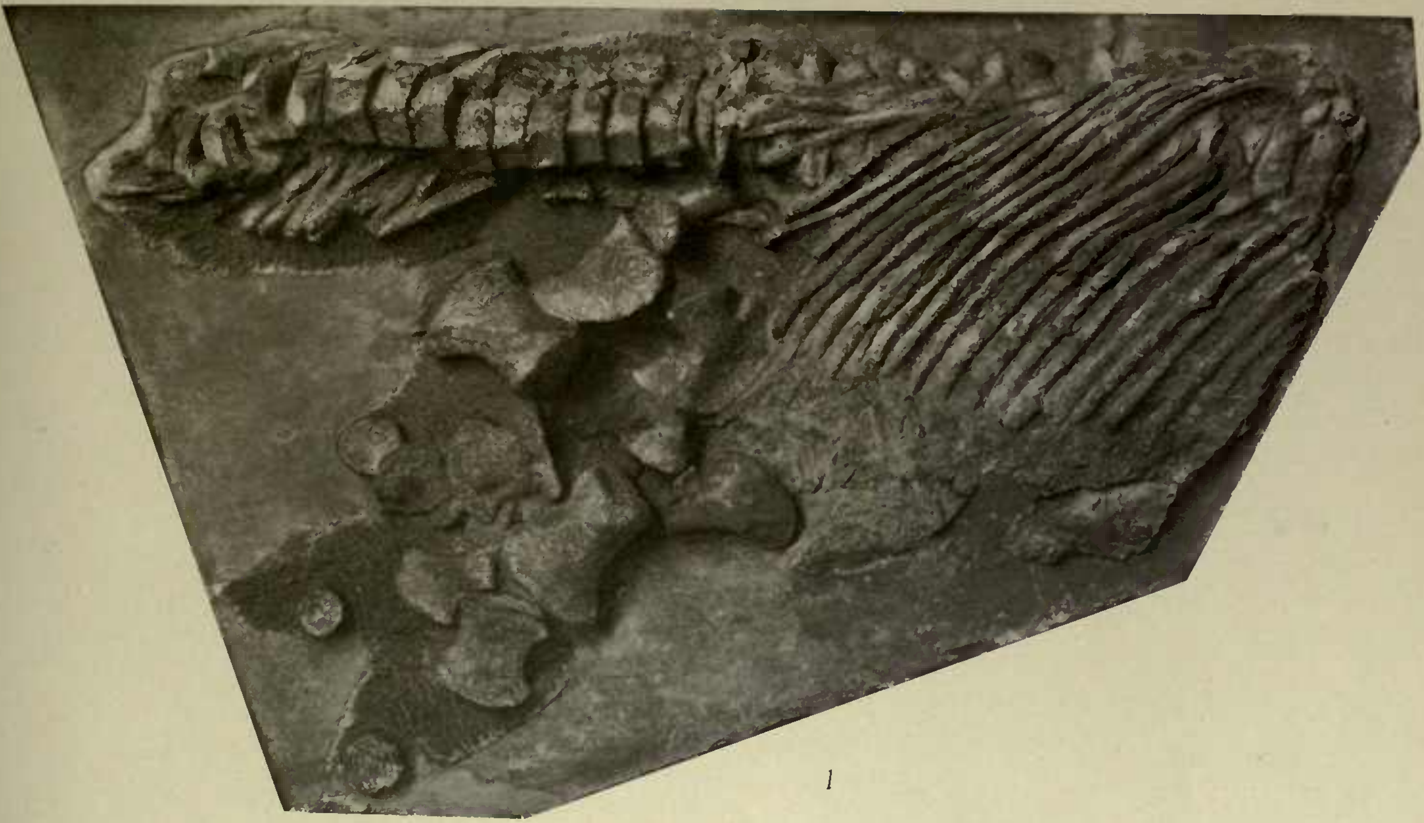
PLATE 17.

EXPLANATION OF PLATE 17.

Fig. 1. *Shastasaurus osmonti* Merriam. Posterior dorsal, pelvic and anterior caudal regions, with elements of posterior arch and limbs, no. 9608, about 1/7 of natural size.

Fig. 2. *Delphinosaurus perrini* Merriam. Elements of posterior arch and limbs, no. 9119, × 3/10.

Fig. 3. *Shastasaurus pacificus* Merriam. Pubis of type specimen, about 3/10 of natural size.



1

2

3

PLATE 18.

EXPLANATION OF PLATE 18.

All specimens from the Upper Triassic of Shasta County, California.
All figures four-ninths of natural size.

Fig. 1. *Shastasaurus altispinus* Merriam. Middle dorsal centrum, no. 9083.

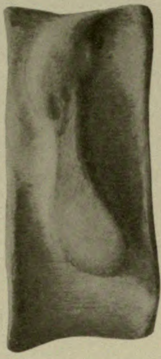
Figs. 2*a* and 2*b*. *Shastasaurus altispinus* Merriam. Neural arch of dorsal vertebra, no. 9083. 2*a*, lateral view; 2*b*, anterior view.

Figs. 3*a* and 3*b*. *Shastasaurus altispinus* Merriam. Head of a right dorsal rib, no. 9083. 3*a*, articular face; 3*b*, posterior side.

Fig. 4. *Shastasaurus altispinus* Merriam. Element from podial region, no. 9083.

Figs. 5*a*, 5*b*, and 5*c*. *Shastasaurus careyi* (?) Merriam. Middle dorsal vertebra, no. 9614. 5*a*, lateral view of vertebra; 5*b*, top of neural spine; 5*c*, anterior view of neural arch.

Fig. 6. *Shastasaurus careyi* (?) Merriam. Posterior view of a dorsal rib, no. 9614.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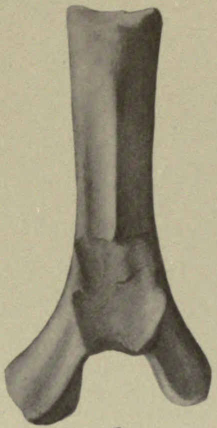
2a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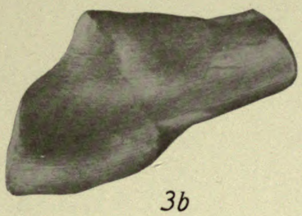
3a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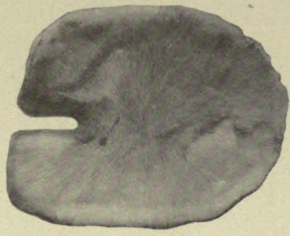
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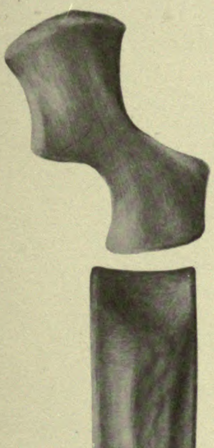
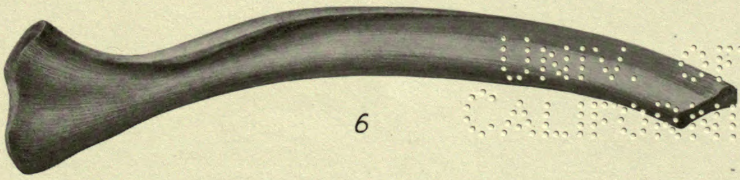

5a


5b


5c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